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Fire Danger Computations with the Hewlett-Packard HP-71B Calculator

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RESEARCH SUMMARY

A fire danger Custom Read Only Memory (CROM) has been developed for the Hewlett-Packard model 71B handheld calculator. This calculator replaces the Texas Instruments TI-59 and can be used in either office or field situations to compute the 1978 National Fire-Danger Rating (NFDR) indexes and components. A separate CROM was developed and a user's manual is being written for calculating several variables to estimate wildfire behavior (Susott and Burgan 1986).

The program reported on here can perform NFDR calculations in two modes: (1) compute NFDR indexes and components from standard NFDRS weather observations, and (2) compute NFDR indexes and components using direct entry of the input data.

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INTRODUCTION

The Hewlett-Packard HP-71B has been selected to replace the Texas Instruments TI-59 (Burgan 1979) for field computations of fire danger and fire behavior. For the TI-59, both fire danger and fire behavior computations were implemented in a single Custom Read Only Memory (CROM). These programs, and their associated users' manuals, have been separated for the HP-71B. This manual describes use of the HP-71B to calculate indexes and components of the 1978 National Fire-Danger Rating (NFDR) System (Deeming and others 1977). Operation of a separate program written for field-oriented fire behavior applications will be described in a companion publication, "Fire Behavior Computations with the Hewlett-Packard HP-71B Calculator" (Susott and Burgan 1986). Each program is available as a separate Custom Read Only Memory.

Separate self-study guides have been prepared for the fire danger and fire behavior programs. These are available through agency coordinators who will distribute the guides and help answer questions about the calculator and course material.

CALCULATOR FEATURES

The HP-71B has several features that make it more suitable for field use than the TI-59 it replaces:

- A liquid crystal display (LCD) that is easy to read in daylight.
- The capability to display both alphabetic and numeric characters. Requests for input and displayed output can now be appropriately labeled, thus eliminating the need for keyboard overlays.
- Use of complementary metal oxide semiconductor (CMOS) architecture which, because of its very low power requirement, permits many hours of operation between battery changes.
- Use of replaceable rather than rechargeable batteries.
- A continuous memory that retains the information stored in the calculator even when the calculator is turned off.
- A capability to operate with optional battery-operated printers, data cassettes, and disk drives.
- A powerful BASIC programming language that is available for many other user applications.

PROGRAM FEATURES

The 1978 NFDR program implemented on the HP-71B performs the same calculations as the TI-59 NFDR program. That is, no changes have been made in the computational algorithms. Highlights of the HP-71B program are:

- NFDR indexes and components can be calculated from either weather data recorded at basic observation time (WEATHER option) or from direct entry of fuel moistures and limited station data (DIRECT option).
- The current 20 NFDR fuel models are included in the CROM, so no fuel model cards are necessary.
- Up to five user-defined fuel models can be stored. Such models may be either a modification of an existing NFDR fuel model or may be developed from entirely new data. Caution is strongly advised in the use of this feature. There is **no** fuel modeling system available for analyzing NFDR fuel models. The fuel modeling subsystem of BEHAVE (Burgan and Rothermel 1984) **cannot** be used to build NFDR fuel models. Without proper analysis, misleading fuel models can easily be built. This feature is primarily for use in fire planning by those trained in fuel modeling.
- Although the program defines a specific sequence for entering data and obtaining calculated results, if inappropriate for your use, both the input and output sequences can be reordered. Specific instructions for reordering sequences can be obtained from: NFDR Liaison, Boise Interagency Fire Center, 3905 Vista Avenue, Boise, ID 83705.
- An automatic update capability is available for those daily inputs whose values must be carried forward. The continuous memory of the HP-71B will retain these and other values even when the calculator is turned off. The automatic update feature may easily be switched on and off.
- The program checks neither the completeness nor the correctness of the inputs. But the program will not accept values outside a reasonable range assigned each input item. Users must be certain that inputs are correct before computing the NFDR indexes and components. If there is any question about this, inputs should be listed before the program is run. The inputs and outputs are stored in continuous memory, so there will **always** be some value—good or bad—assigned to the inputs.

• All critical values from the most recent run are automatically saved in a file called DSTATE. (Other files used by this program—NFDR, MODELS, NAMES—are in the fire danger custom module.) The DSTATE file is updated after each run in DIRECT and WEATHER, after a fuel model is "saved," and when you "quit" the NFDR program completely. These values are read back in from the DSTATE file at the beginning of each run. This eliminates the possibility of any NFDR data being altered if the HP-71B is used for either manual calculations or another program application. Operation of the NFDR program will not alter any values assigned to variables created in other programs and saved in continuous memory. Some global flags and default values are changed during operation, including flags 0 through 8, DELAY 0, 0, OPTION ROUND NEAR, OPTION BASE 1, OPTION ANGLE RADIANS, and display format STD. Refer to the HP-71 Reference Manual for more information about these values.

• The 1,000-hour timelag fuel moisture (1000 HRFM) calculation is the same as used for the TI-59. To enhance user convenience, it differs slightly from the calculations done by AFFIRMS (Helfman and others 1980).

• Relative humidity is required rather than dewpoint or dry bulb and wet bulb temperatures.

• Fuel-stick moisture adjustments for aging must be done before using the NFDR program.

PROGRAM STRUCTURE

The NFDR program structure consists of a MAIN section that contains three modules—MODEL, DIRECT, and WEATHER—and two primary commands—PRINTER and QUIT. Several second-level keyword commands are available within each of the three modules (appendix A). Control of program operation is through the use of one-letter keywords to select a module or perform one of the keyword commands. These are the underlined letters in appendix A. Once a module is selected, its keywords are operative and will appear in the display. You can switch from one module to another only by going through the MAIN section. For example, if you were using the DIRECT module and wanted to go to the WEATHER module, you would have to Quit DIRECT, thus getting back to the MAIN section, from which you could select the WEATHER module. The Printer keyword will alternately direct I/O to the printer or to the display when used repeatedly. If a printer is not attached to the calculator or is attached but not turned on, use of this keyword will only result in display of the message "NO PRINTER AVAILABLE". The NFDR program should always be ended by entering Q for Quit while in the MAIN section to properly save your current data and return the calculator to normal use.

OPERATION OF THE "MAIN" SECTION

After the HP-71B has been turned on, the NFDR program can be started in either of two ways:

1. Type in RUN NFDR and press the ENDLINE key. This will always work even if the program has been paused.

2. If the NFDR program was the last program run before the calculator was turned off, just press the RUN key.

When the program starts running, PRGM will appear in small letters on the right side of the display. This is followed immediately by a short display of the words "FIRE DANGER". The program then searches to determine whether or not a printer is attached to the calculator. If a printer is attached **and turned on**, the message "PRINTER ON" is briefly displayed; otherwise the message "NO PRINTER AVAILABLE" is briefly displayed. Finally, the program indicates you are in the MAIN section by displaying the module and keyword message "MAIN: M,D,W,P,Q?" At this point, you can go to one of the modules—Model, Direct, or Weather, toggle the Printer or Quit by entering the appropriate letter in the display, and pressing ENDLINE. If you press any other letter, a number or a symbol, and ENDLINE, the incorrect entry will just disappear and you can try again.

Operation of the fire danger program uses some of the HP-71B memory. Large user files or previously defined variables can cause the "Insufficient Memory" error at unpredictable locations in the program. The "DESTROY ALL" statement may reclaim enough memory to run the program, or files can be removed with the "PURGE" statement. Users who frequently have large files in memory should consider obtaining the optional memory expansions available for the HP-71B.

Erroneous entries can be corrected before the ENDLINE key is pressed by:

1. Holding down the gold f key and either pressing the < key repeatedly or else holding the < key down. This invokes the "BACK" command printed in gold letters on the calculator.

2. Pressing or holding the < key to back up the cursor, then deleting the unwanted characters by pressing or holding the f key and then the > key. This invokes the "−CHAR" command.

3. Using the < key to back up the cursor, then typing in the correct inputs. If extra characters remain, they can be deleted individually by pressing the f and > keys, or all at once ("−LINE" command) by pressing the f and V keys.

Refer to the HP-71B User's Manual for more detailed line-editing instructions.

Normal termination of the NFDR program is with use of the keyword Quit when you are in the MAIN section. This ensures that current program variables are saved. Although it is not recommended, you may turn the calculator off any time the program waits for user input, by pressing f ON to invoke the "OFF" command. The calculator will also automatically turn off if there is no user activity for 10 minutes. In these cases, when the calculator is turned back on, the SUSP annunciator will appear in the display, indicating program operation is now suspended. To continue from this point, press f +

for the "CONT" or continue command, and a question mark "?" will appear. The calculator is now waiting for you to input the value for the item being requested when the calculator was turned off. If you don't know what to enter, press the + (plus sign), ENDLINE and the display will then show the input being requested when the calculator was turned off. Check your inputs and correct any erroneous values before continuing. Turning the calculator off while it is doing calculations may result in loss of data and leave some calculator keys inoperable. If this happens, enter "RUN NFDR" and Quit when the display reads "MAIN: M,D,W,P,Q?". Then the calculator keys will operate normally again.

INPUT AND OUTPUT PROCEDURES

Definition of Inputs

The following tabulation defines the inputs and provides instructions concerning values used in operating the WEATHER module.

All three modules—MODEL, DIRECT, and WEATHER—employ the same techniques for data entry and modification.

The inputs and outputs for each module have been numbered and arranged in a specific sequence. If you modify the order of the input/output lists of appendix B, the line numbers will still be sequential (1,2,3,...), but different input and/or output items will be associated with them. The item numbers provide much flexibility in data entry, listing, and output of results.

Entry	Mnemonic	Item	Instructions
1	UPDATE	Auto updating	No for first day, then Yes
2	MONTH	Month of year	Enter as a whole number
3	DAY	Day of month	Enter as a whole number
4	GREEN DAYS	Green days	Prior to greening or after a freeze use 0. Enter 1 on the day green-up begins, 2 on the second day of green-up, 3 on the third, and so on. Continue entering successively higher numbers until **both** herbaceous and woody vegetation go dormant as a result of a freeze, drought, or seasonal cycle; then use 0 again.
5	STATE WTHR	State of the weather	Enter as whole number 0-9
6	TEMP	Dry bulb temperature	Enter in degrees fahrenheit
7	RH	Relative humidity	Enter directly. Cannot be calculated from wet bulb temperature.
8	10 HRFM	Observed fuel sticks	If not known, enter 2 to obtain a calculated value.
9	WINDSPEED	20-foot windspeed	Enter in miles per hour
10	MAX TEMP	Maximum temperature	Enter in degrees fahrenheit
11	MIN TEMP	Minimum temperature	Enter in degrees fahrenheit
12	MAX RH	Maximum relative humidity	Enter in percent
13	MIN RH	Minimum relative humidity	Enter in percent
14	PRECIP DUR	Precipitation duration	Enter to nearest whole hour
15	Y-100 HRFM	Yesterday's 100-hour moisture	For the first day's calculations use 10, 15, 20, or 25 for climate classes 1, 2, 3, or 4, respectively.
16	Y-1000 HRFM	Yesterday's 1,000-hour moisture	For the first day's calculations use 15, 20, 25, or 30 for climate classes 1, 2, 3, or 4, respectively.
17	Y-X1000 HRFM	Yesterday's X1,000 moisture	For the first day's calculations use the value for Y-1000 HRFM as described above.
18	Y-HERB FM	Yesterday's herb moisture	For the first day's calculations use your best estimate.
19	MAN RISK	Man-caused risk	Determine as instructed in the National Fire-Danger Rating System—1978 (Deeming and others 1977) and enter the value for today.
20	LGT ACT LVL	Lightning activity level	Determine as instructed in the National Fire-Danger Rating System—1978 (Deeming and others 1977) and enter the value for today.
21	Y-LGT OCC	Yesterday's lightning occurrence	For the first day's calculations use 0
22	FUEL MODEL	Fuel model name	Enter letter for appropriate model
23	LATITUDE	Station latitude	Enter to nearest whole degree
24	SLOPE CLASS	Slope class	Enter slope class assigned to station
25	CLIM CLASS	Climate class	Enter climate class assigned to station
26	LRSF	Lightning risk scaling factor	Enter value assigned to station

The inputs are limited to reasonable ranges as listed on the worksheets. If you have not assigned a value to a required input item, the minimum value of the range for that item will automatically be assigned and used.

Entering and Listing Inputs

To enter or list input items, you can

- Begin entering or listing data at the first item in the list by entering I or L, respectively.
- Begin entering or listing data at any item number by entering I# or L#, respectively, where # is the item number. A space between L and # is optional. For example, entering I4 when the display reads WEATHER: I,L,R,Q will allow you to enter green days (fourth item in the weather input list). Entering I4 when the display reads DIRECT: I,L,R,Q will allow entry of 100-hour fuel moisture (fourth item in the DIRECT list).

Once you have started entering input data at some point in the input list, you can continue sequentially from there. Entry of data can be terminated at any time by pressing ENDLINE without first keying in an entry. This will not affect the input parameter whose value is being requested.

Similarly, input listing can be started at any point by entering L#. Subsequent items can be listed by pressing the V key. Previous items can be listed by pressing the Λ key. Terminate the listing by pressing ENDLINE. When a printer is attached, there is no pause between list items, and all remaining items will be printed.

Changing Inputs

The value of individual input items can be changed by entering I# where # is the number of the input parameter to be changed. The display will show the mneumonic and range for that item number. Enter the value and press ENDLINE. The next input item will then appear in the display, but if you do not want to change its value, press ENDLINE .

Obtaining Outputs

After you are certain the input values are correct, outputs from a DIRECT or WEATHER run may be obtained by:

- Entering R to start at the beginning of the output list.
- Entering R# to start at the location of the item number specified.

If you are not using a printer, you may scroll up or down the output list by repeatedly pressing the Λ or V keys, respectively. Output listing is terminated by pressing ENDLINE. If the output is going to a printer, the Λ, V and ENDLINE keys are deactivated and the list is printed from your starting point to the end of the list.

In some applications, it may be convenient to avoid computation of the man-caused occurrence index (MCOI) and/or lightning risk (LRISK) and lightning occurrence index (LOI). If man-caused risk (MAN RISK) is entered as zero, the man-caused occurrence index will not be output. If the lightning risk scaling factor (LRSF) is zero, neither lightning activity level (LGT ACT LVL) nor yesterday's lightning occurrence index (Y-LGT OCC) inputs will be requested, nor will LRISK or LOI be output. If both MAN RISK and LRSF are zero, none of the above outputs will be calculated.

MAN RISK is part of the daily input list, so you can always enter a nonzero value. But the LRSF is at the bottom of the input list as part of the station data. It was placed there because it normally does not change, so there is no reason to ask for it daily. So, if the LRSF is set to zero and you want the lightning related outputs, first change it to a nonzero value by entering an LRSF value individually, then begin normal data entry. If LRSF is not zero, LGT ACT LVL and Y-LGT OCC inputs will be requested and LRISK and LOI will be output.

Thus, any of four output lists may be selected in either the DIRECT or WEATHER modules as follows:

- List 1 - a complete list of all eight NFDR indexes and components, obtained by entering valid data for all the inputs
- List 2 - elimination of the man-caused occurrence index (MCOI) by entering zero for man-caused risk (MAN RISK)
- List 3 - elimination of lightning risk (LRISK) and the lightning occurrence index (LOI) by entering zero for the lightning risk scaling factor (LRSF)
- List 4 - elimination of MCOI, LRISK, and LOI by entering zero for both MAN RISK and LRSF

OPERATION OF THE "MODEL" MODULE

The purpose of this module is to permit the modification of an existing NFDR fuel model or the entry of an entirely new one. Because of the difficulty of building reliable fuel models, we suggest user models be built by slightly modifying existing NFDR models rather than developing entirely new models. An example of this is switching herbaceous type between annual and perennial Fire danger indexes cannot be calculated with this module—it is strictly for modifying and saving user models.

When the calculator display shows - MODEL: G,I,L,S,Q? - you are in the MODEL module and may:

- <u>G</u>et an NFDR model (A-U except M) or an existing user model (V-Z) by entering G and a model letter. For example, if the display shows - MODEL: G,I,L,S,Q? - you can get model B by entering GB and pressing ENDLINE. The display will flash "MODEL B LOADED". If you just enter G, the program will request a model by displaying "FUEL MODEL (A-Z)?".

Because NFDR model M does not exist, an attempt to load it by entering GM will result in another request for the model, as above. If an M is entered at this point, it will just disappear when ENDLINE is pressed, and no model will be loaded. Either enter a valid model letter or just ENDLINE to return to the module prompt.

If you try to <u>G</u>et a user model that does not exist, the calculator will display "MODEL NOT IN FILE", and

request another input. Get will load only user models (V–Z) if they have been filed using a Save command.

• Input all the data for a new model by entering I when the display shows - MODEL: G,I,L,S,Q? The program recognizes that some inputs are not always required. For example, if the WOOD LOAD is entered as zero, the WOOD S/V ratio input will not be requested. HERB TYPE and HERB S/V ratio are similarly linked to HERB LOAD.

• Input individual parameters by referring to their line numbers. For example, I3 will cause the calculator to request a value for 10 HR LOAD, the third item in the model input list. This procedure will allow input of HERB and WOOD S/V ratios and HERB TYPE even if they are not needed. The values assigned to unneeded inputs are saved in the user file DSTATE, but they have no effect on calculations made in DIRECT or WEATHER.

• List the current values from the beginning (by entering L) or from any other location in the list by entering a line number with the L; for example, L3.

• Save a model in the "USERMOD" fuel model file, which the program automatically creates for you.

• Quit the MODEL module.

As mentioned previously, both input and list can be terminated by pressing ENDLINE without first keying in an entry.

If you just Get an NFDR model and try to Save it without giving it another name, you will be asked to name the model (V–Z) because you cannot save a model named A–U. If you attempt to save a model named V–Z and one already exists in the USERMOD file, you will be asked whether or not you want to "KILL OLD MODEL (Y/N)?". This gives you the options of assigning a different name, not saving the model, or saving over an existing fuel model. You can also Save a model by typing S and a model letter (V–Z), then pressing ENDLINE; for example, SV ENDLINE.

When you save a model by entering Save after inputting values for one or more fuel model parameters, the calculator will automatically calculate and display the maximum probable spread rate (SCM) as calculated using the following environmental conditions:

1-hour fuel moisture	4%
10-hour fuel moisture	6%
100-hour fuel moisture	8%
1,000-hour fuel moisture	11%
Herbaceous fuel moisture	65%
Woody fuel moisture	75%
Windspeed (20-ft)	20 mi/h
Slope class	1 (22.5% slope)
Climate class	3

The SCM value is used in calculating the ignition component (IC). Write the SCM value on the fuel model form and press ENDLINE to continue. The entire model will then be stored in the USERMOD file.

Any fuel model you "Get" or build in this module will also be assigned to the DIRECT and WEATHER modules. But both DIRECT and WEATHER also allow you to assign a fuel model. A fuel model assigned in any one of the three modules is automatically assigned to the other two modules.

OPERATION OF THE "WEATHER" MODULE

An update option included in this module provides the choice of whether or not to automatically update those input items whose values must be carried forward from day to day. The updatable items are 100-hour fuel moisture (100 HRFM), 1,000-hour fuel moisture (1000 HRFM), X1,000 moisture (X1000 HRFM), live herbaceous moistures (HERB FM), and the lightning occurrence index (LOI). The "UPDATE" option is available in the WEATHER module only. Selection of UPDATE (Y/N) is the first item in the weather input list.

To establish valid starting values at the beginning of a fire season, set UPDATE to No, enter the first day's weather data (items 2-21), the station data (items 22-26), complete the run, and record the results. Then Input line 1 and change UPDATE to Yes. Daily NFDR runs can then be made by just selecting the WEATHER module, entering the current day's data, and completing the run. You will not be queried for the updatable items unless you change UPDATE to No to permit manual entry.

Input of any WEATHER module input item **except** the UPDATE input itself (Y or N) or fuel model, **will change** the values of the updatable items as long as UPDATE is set to Yes. But you can run multiple fuel models with UPDATE set to Yes without altering the values of the updatable items. This is a feature to allow use of the current day's weather to calculate NFDR indexes and components for several fuel models. The same slope and climate class should be associated with these models. If they are not, the weather data is probably not representative, and the fuel moistures may not be appropriate. For models run in this manner, you must be **absolutely certain** that the live herbaceous fuel load, if present, is designated as either annual (herb type 1) or perennial (herb type 2). Otherwise, you will erroneously use the moisture content calculated for annuals, in the computations for models containing perennials, or vice versa. Model A is the only **standard** NFDR fuel model designated as having annual herbaceous vegetation; however, you may create user models (V–Z) having either annual or perennial vegetation.

Fire danger computations should begin while the previous year's herbaceous vegetation is still "cured." In this situation, keep entering green days as Ø until greenup starts. Then begin incrementing the green day's value by 1 each day. This will cause the live herbaceous moisture to begin increasing to some maximum value, depending on other daily weather data entered as the season progresses, and then begin decreasing when summer drying begins. As drying continues, the moisture content of "annual" herbaceous vegetation will gradually decrease to 30 percent, at which point it will be considered completely cured and herbaceous fuel moisture will automatically be set equal to the 1 HRFM.

The moisture content of "perennial" herbaceous vegetation will increase and decrease in response to wetting and drying cycles. It will not decrease below 30 percent unless you force it to a "cured" state by entering a

green day's value of Ø. This will cause the value for moisture content of perennial herbaceous vegetation to be set equal to the 1 HRFM.

Example "WEATHER" Runs

Two example weather runs will illustrate:

1. Entering data and obtaining output for the first day of a fire season.

2. Entering data and obtaining output for the second and subsequent days' NFDR calculations.

Select the WEATHER module and Input, then List the data for day 1 in the following tabulation (exhibit 1). Run the program and verify the outputs. Set UPDATE to Yes, enter and list data for day 2, then Run the program, and verify the outputs. Example printer output for these two runs is provided (exhibits 2 and 3).

Exhibit 1.—Example WEATHER module inputs and outputs for 2 days.

SAMPLE NFDR WEATHER OPTION DATA FORM

Name ______ Date ______ Sheet ______ of ______

INPUTS

Line Number	Mnemonic	Item	Range	Value		
1	UPDATE	Update	(Y/N)	N	Y	
2	MONTH	Month	(1-12)	5	5	
3	DAY	Day	(1-31)	29	30	
4	GREEN DAYS	Green days	(0-366)	0	1	
5	STATE WTHR	State of weather	(0-9)	3	3	
6	TEMP	Dry bulb temperature	(0-120°F)	69	54	
7	RH	Relative humidity	(0-100%)	34	66	
8	10 HRFM	[1]10-hour fuel moisture	(2-50%)	10	13	
9	WINDSPEED	20-foot windspeed	(0-60 mi/h)	7	2	
10	MAX TEMP	Maximum temperature	(0-120°F)	71	70	
11	MIN TEMP	Minimum temperature	(0-120°F)	31	43	
12	MAX RH	Maximum relative humidity	(0-100%)	99	99	
13	MIN RH	Minimum relative humidity	(0-100%)	18	50	
14	PRECIP DUR	Precipitation duration	(0-24 hours)	0	1	
15	Y-100 HRFM	Yesterday's 100-hour moisture	(2-50%)	12.29	U[4]	
16	Y-1000 HRFM	Yesterday's 1000-hour moisture	(2-50%)	20.95	U[4]	
17	Y-X1000 HRFM	Yesterday's X1000 moisture	(2-50%)	20.95	U[4]	
18	Y-HERB FM	Yesterday's herb moisture	(2-50%)	7	U[4]	
19	MAN RISK	[2]Man-caused risk	(0-100)	1	15	
20	LGT ACT LVL	Lightning activity level	(1-6)	1	2	
21	Y-LGT OCC	Yesterday's lightning occurrence	(0-100)	1	ENDLINE	
22	FUEL MODEL	Fuel model name	(A-Z)	G		
23	LATITUDE	Latitude	(−67 to 67°)	48		
24	SLOPE CLASS	Slope class	(1-5)	3		
25	CLIM CLASS	Climate class	(1-4)	3		
26	LRSF	[3]Lightning risk scaling factor	(0-1)	1.0		

(con.)

SAMPLE NFDR WEATHER OPTION DATA FORM (Con.)

Name ______________________ Date ____________ Sheet ______ of ______

OUTPUTS

Line Number	Mnemonic	Item	Units	Value		
	Indexes and Components					
1	SC	Spread Component		11	5	
2	ERC	Energy Release Component		28	24	
3	BI	Burning Index		42	28	
4	IC	Ignition Component		21	5	
5	MCOI	[2]Man-Caused Occurrence Index		0	1	
6	LRISK	[3]Lightning Risk		0	13	
7	LOI	[3]Lightning Occurrence Index		0	1	
8	FLI	Fire Load Index		30	20	
	Moistures					
9	1 HRFM	1-hour fuel moisture	(pct)	7.3	12.2	
10	10 HRFM	10-hour fuel moisture	(pct)	10.0	13.0	
11	100 HRFM	100-hour fuel moisture	(pct)	12.29	13.62	
12	1000 HRFM	1000-hour fuel moisture	(pct)	20.57	20.46	
13	X1000 HRFM	X1000 fuel moisture	(pct)	20.57	20.46	
14	WOOD FM	Live woody fuel moisture	(pct)	70	74	
15	HERB FM	Live herbaceous fuel moisture	(pct)	7	20	

[1]If a 10 H moisture is input, that same value will be output, except that it will never be less than 2. If the 10 H moisture is entered as 2, a calculated value will appear in the output list.
[2]If man-caused risk is 0, man-caused occurrence index will not be output.
[3]If the lightning risk scaling factor is 0, lightning risk and lightning occurrence index will not be output.
If both man-caused risk and lightning risk scaling factor are zero, man-caused occurrence index, lightning risk, and lightning occurrence index will not be output.
[4]Updatable items not requested because UPDATE is set to **Yes**.

Exhibit 2.—Example printer output—first day.

1	UPDATE	N
2	MONTH	5
3	DAY	29
4	GREEN DAYS	0
5	STATE WTHR	3
6	TEMP	69
7	RH	34
8	10 HRFM	10.0
9	WINDSPEED	7
10	MAX TEMP	71
11	MIN TEMP	31
12	MAX RH	99
13	MIN RH	18
14	PRECIP DUR	0.00
15	Y-100 HRFM	12.29
16	Y-1000 HRFM	20.95
17	Y-X1000 HRFM	20.95
18	Y-HERB FM	7
19	MAN RISK	1
20	LGT ACT LVL	1
21	Y-LGT OCC	1
22	FUEL MODEL	G
23	LATITUDE	48
24	SLOPE CLASS	3
25	CLIM CLASS	3
26	LRSF	1.00

1	SC	11
2	ERC	28
3	BI	42
4	IC	21
5	MCOI	0
6	LRISK	0
7	LOI	0
8	FLI	30
9	1 HRFM	7.3
10	10 HRFM	10.0
11	100 HRFM	12.29
12	1000 HRFM	20.57
13	X1000 HRFM	20.57
14	WOOD FM	70
15	HERB FM	7

In normal daily operation, the calculator will be turned on, the WEATHER module selected, and either I2 or I3 entered to begin inputs at month or day, respectively. Inputs do not have to begin at UPDATE (I1) unless you want to change the UPDATE setting. Multiple fuel models all having the same herb type can be run with UPDATE set to Yes by entering I22, fuel model, then pressing ENDLINE and Run. Verify this by entering I22, fuel model C, ENDLINE when latitude is requested, and then Run. Note that the NFDR index and component values changed from the results of the day 2 run, but the moisture outputs did not. Then enter model G again (I22, G), press ENDLINE to terminate inputs, and do another run. All the outputs will exactly match the day 2 run. This illustrates the procedure for running multiple fuel models with the same weather data.

Exhibit 3.—Example printer output—second day.

1	UPDATE	Y
2	MONTH	5
3	DAY	30
4	GREEN DAYS	1
5	STATE WTHR	3
6	TEMP	54
7	RH	66
8	10 HRFM	13.0
9	WINDSPEED	2
10	MAX TEMP	70
11	MIN TEMP	43
12	MAX RH	99
13	MIN RH	50
14	PRECIP DUR	1.00
15	Y-100 HRFM	12.29
16	Y-1000 HRFM	20.57
17	Y-X1000 HRFM	20.57
18	Y-HERB FM	7
19	MAN RISK	15
20	LGT ACT LVL	2
21	Y-LGT OCC	0
22	FUEL MODEL	G
23	LATITUDE	48
24	SLOPE CLASS	3
25	CLIM CLASS	3
26	LRSF	1.00

1	SC	5
2	ERC	24
3	BI	28
4	IC	5
5	MCOI	1
6	LRISK	13
7	LOI	1
8	FLI	20
9	1 HRFM	12.2
10	10 HRFM	13.0
11	100 HRFM	13.62
12	1000 HRFM	20.46
13	X1000 HRFM	20.46
14	WOOD FM	74
15	HERB FM	20

If UPDATE is to be changed from its previous setting, change it **first**, before entering any other data. It is placed first in the input list for convenience. Notice that when UPDATE was set to Yes in day 2, the updatable items (yesterday's values) were not asked for. In addition, if the station parameters (items 22-26) do not change, input can be terminated by pressing ENDLINE when a fuel model is requested.

If your daily calculations get "off track" because of some prior erroneous input, you can restart the calculations from the most recent date for which you have recorded correct results. Follow the procedures described previously for starting at the beginning of a session, but be aware that the GREEN DAYS value should be appropriate for the month and day of the midseason startup.

OPERATION OF THE "DIRECT" MODULE

The purpose of the DIRECT module is to permit calculation of NFDR indexes and components from direct entry of fuel moisture rather than moisture values calculated from weather inputs. This provides a "gaming" flexibility for use in research, training, or planning.

Example "DIRECT" Runs

Exhibit 4 gives an example of two runs to illustrate use of the DIRECT module to obtain both a full output list and an optional shortened output list. Select the DIRECT module, enter the data, and run each example in turn. Only outputs 1-4 and 8 are obtained in the second run in exhibit 4 because both the Man-caused Risk and the Lightning Risk Scaling Factor were entered as zero. Zero does not need to be entered for either MCR or LRSF more than once. Enter these values again only if you want to change them; otherwise, terminate input by pressing ENDLINE when these inputs are requested.

In DIRECT, state of weather and temperature **do not** affect the fuel moistures; however, they do affect the Ignition Component and the outputs which are in turn affected by the Ignition Component.

Exhibit 4.—Example DIRECT module inputs and outputs for two typical runs.

SAMPLE NFDR DIRECT OPTION DATA FORM

Name ______________ Date ______________ Sheet ______ of ______

INPUTS

Line Number	Mnemonic	Item	Range	Value		
1	FUEL MODEL	Fuel model name	(A-Z)	S	H	
2	1 HRFM	1-hour fuel moisture	(2-50%)	7	9	
3	10 HRFM	10-hour fuel moisture	(2-50%)	8	10	
4	100 HRFM	100-hour fuel moisture	(2-50%)	10	11	
5	1000 HRFM	1000-hour fuel moisture	(2-50%)	12	13	
6	WOOD FM	Live woody fuel moisture	(30-200%)	95	110	
7	HERB FM	Live herbaceous fuel moisture	(2-250%)	90	100	
8	WINDSPEED	20-foot windspeed	(0-60 mi/h)	5	10	
9	SLOPE CLASS	Slope class	(1-5)	1	3	
10	STATE WTHR	State of weather	(0-9)	0	0	
11	TEMP	Temperature	(0-120°F)	80	85	
12	MAN RISK	[1]Man-caused risk	(0-100)	10	0	
13	LRSF	[2]Lightning risk scaling factor	(0-1)	0.8	0	
14	Y-LGT OCC	Yesterday's lightning occurrence	(0-100)	24	–	
15	LGT ACT LVL	Lightning activity level	(1-6)	2	–	

OUTPUTS

	Indexes and Components				
1	SC	Spread Component	2	3	
2	ERC	Energy Release Component	14	20	
3	BI	Burning Index	15	18	
4	IC	Ignition Component	16	18	
5	MCOI	[1]Man-Caused Occurrence Index	2	–	
6	LRISK	[2]Lightning Risk	10	–	
7	LOI	[2]Lightning Occurrence Index	9	–	
8	FLI	Fire Load Index	13	13	

[1]If man-caused risk is 0, man-caused occurrence index will not be output.
[2]If the lightning risk scaling factor is 0, lightning risk and lightning occurrence index will not be output.
If both man-caused risk and lightning risk scaling factor are zero, man-caused occurrence index, lightning risk, and lightning occurrence index will not be output.

COMMUNICATION BETWEEN WEATHER AND DIRECT

All the inputs **except** "yesterday's" inputs are common to both WEATHER and DIRECT, that is, they are "known" to both modules. These are: FUEL MODEL, 1-, 10-, 100-, 1000-HR, HERB and WOOD moistures, wind, slope class, state of weather, temperature, man-caused risk, lightning risk scaling factor, and lightning occurrence level. Thus, if any of these values are set in DIRECT, they will also be set in WEATHER and vice versa. This feature permits the use of WEATHER to calculate fuel moistures for DIRECT. Then DIRECT can be used to determine how the NFDR indexes and components change as other DIRECT inputs are varied. If you were to then switch back to WEATHER and run it without inputting a new set of weather data, the values of the most recent DIRECT run would be used by WEATHER. But normally you would input new weather data before running the WEATHER module. The new weather input, along with the fact that none of the "yesterday's" values are changed by DIRECT, assure correct output for the next weather run.

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Burgan, Robert E. Fire danger/fire behavior computations with the Texas Instruments TI-59 calculator: user's manual. General Technical Report INT-61. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1979. 25 p.

Burgan, Robert E.; Rothermel, Richard C. BEHAVE: fire behavior prediction and fuel modeling system—FUEL subsystem. General Technical Report INT-167. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1984. 126 p.

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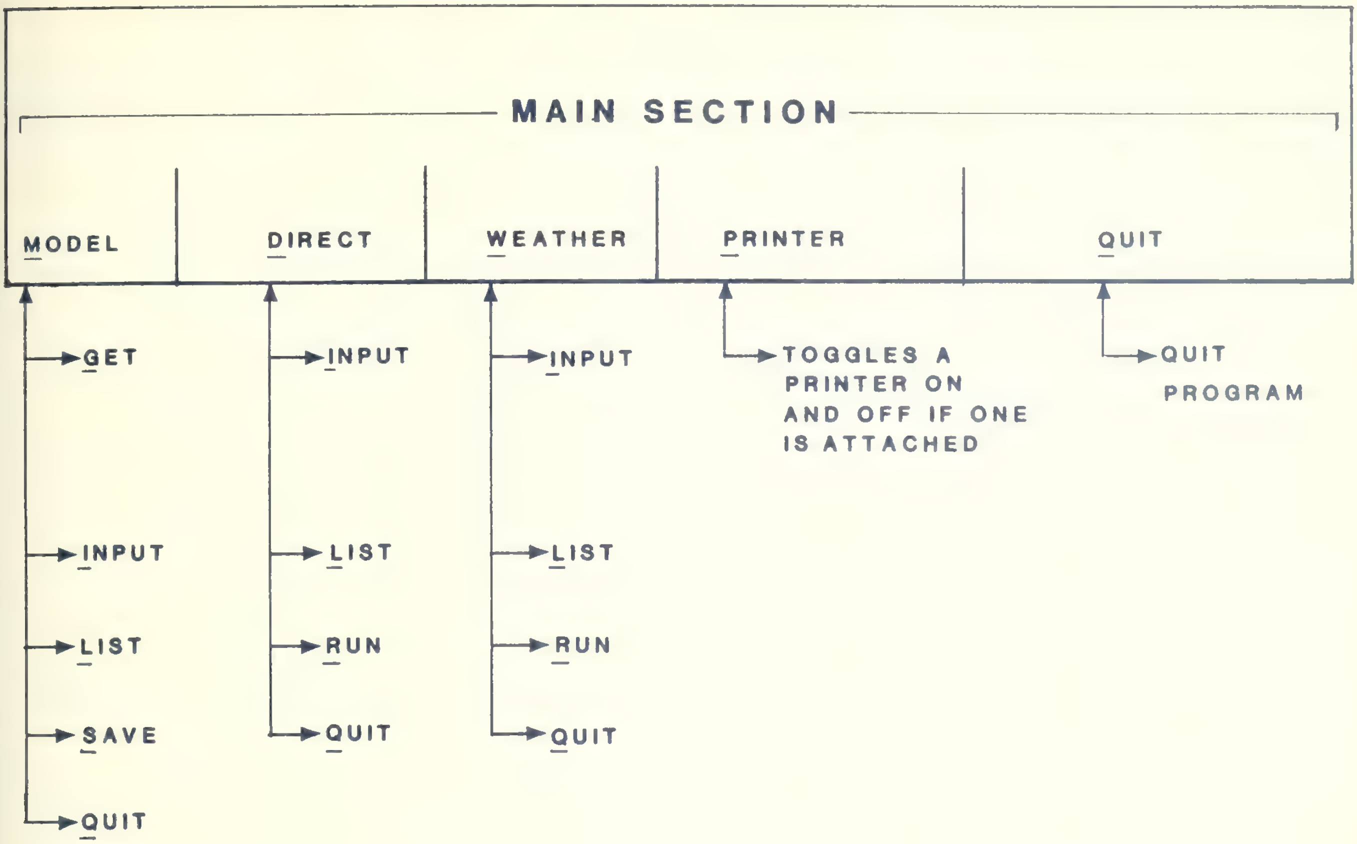
Helfman, Robert S.; Straub, Robert J.; Deeming, John E. User's guide to AFFIRMS: time-share computerized processing for fire danger rating. General Technical Report INT-82. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980. 150 p.

Susott, Ronald A.; Burgan, Robert E. Fire behavior computations with the Hewlett-Packard HP-71B calculator. General Technical Report INT-202. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986.

APPENDIX A: NFDR PROGRAM STRUCTURE AND KEYWORD LIST



APPENDIX B: SAMPLE DATA FORMS

SAMPLE USER FUEL MODEL FORM

Name ______________________ Date ______________ Sheet ________ of ________

Line Number	Mnemonic	Item	Range	Value
1	FUEL MODEL	Fuel model name	(V-Z)	________
2	1 HR LOAD	1-hour load	(0.01-30 tons/acre)	________
3	10 HR LOAD	10-hour load	(0.0-30 tons/acre)	________
4	100 HR LOAD	100-hour load	(0.0-30 tons/acre)	________
5	1000 HR LOAD	1000-hr load	(0.0-30 tons/acre)	________
6	WOOD LOAD	Live woody load	(0.0-30 tons/acre)	________
7	HERB LOAD	Live herb load	(0.0-30 tons/acre)	________
8	HERB TYPE	Herb type 1 = annual 2 = perennial	(1-2)	________
9	1 HR S/V	1 hr surface/volume ratio	(1200-3500 ft^2/ft^3)	________
10	WOOD S/V	Live woody surface/ volume ratio	(1200-3500 ft^2/ft^3)	________
11	HERB S/V	Live herb surface/ volume ratio	(1200-3500 ft^2/ft^3)	________
12	HEAT	Heat content	(7000-12000 Btu/lb)	________
13	MOIS EXT	Dead fuel moisture of extinction	(10-50%)	________
14	DEPTH	Fuel bed depth	(0.1-10 ft)	________
15	WIND FACTOR	Wind adjustment factor	(0-1)	________
16	SCM	[1]Maximum probable spread component	(0-1000)	________

[1]SCM is automatically calculated when the fuel model is saved. Enter here for reference when it is displayed.

(con.)

SAMPLE NFDR WEATHER OPTION DATA FORM

Name ______________________ Date ____________ Sheet ______ of ______

INPUTS

Line Number	Mnemonic	Item	Range	Value		
1	UPDATE	Update	(Y/N)			
2	MONTH	Month	(1-12)			
3	DAY	Day	(1-31)			
4	GREEN DAYS	Green days	(0-366)			
5	STATE WTHR	State of weather	(0-9)			
6	TEMP	Dry bulb temperature	(0-120°F)			
7	RH	Relative humidity	(0-100%)			
8	10 HRFM	[1]10-hour fuel moisture	(2-50%)			
9	WINDSPEED	20-foot windspeed	(0-60 mi/h)			
10	MAX TEMP	Maximum temperature	(0-120°F)			
11	MIN TEMP	Minimum temperature	(0-120°F)			
12	MAX RH	Maximum relative humidity	(0-100%)			
13	MIN RH	Minimum relative humidity	(0-100%)			
14	PRECIP DUR	Precipitation duration	(0-24 hours)			
15	Y-100 HRFM	Yesterday's 100-hour moisture	(2-50%)			
16	Y-1000 HRFM	Yesterday's 1000-hour moisture	(2-50%)			
17	Y-X1000 HRFM	Yesterday's X1000 moisture	(2-50%)			
18	Y-HERB FM	Yesterday's herb moisture	(2-50%)			
19	MAN RISK	[2]Man-caused risk	(0-100)			
20	LGT ACT LVL	Lightning activity level	(1-6)			
21	Y-LGT OCC	Yesterday's lightning occurrence	(0-100)			
22	FUEL MODEL	Fuel model name	(A-Z)			
23	LATITUDE	Latitude	(−67 to 67°)			
24	SLOPE CLASS	Slope class	(1-5)			
25	CLIM CLASS	Climate class	(1-4)			
26	LRSF	[3]Lightning risk scaling factor	(0-1)			

(con.)

SAMPLE NFDR WEATHER OPTION DATA FORM (Con.)

Name ______________________ Date ______________ Sheet ________ of ________

OUTPUTS

Line Number	Mnemonic	Item	Units	Value		
	Indexes and Components					
1	SC	Spread Component		____	____	____
2	ERC	Energy Release Component		____	____	____
3	BI	Burning Index		____	____	____
4	IC	Ignition Component		____	____	____
5	MCOI	[2]Man-Caused Occurrence Index		____	____	____
6	LRISK	[3]Lightning Risk		____	____	____
7	LOI	[3]Lightning Occurrence Index		____	____	____
8	FLI	Fire Load Index		____	____	____
	Moistures					
9	1 HRFM	1-hour fuel moisture	(pct)	____	____	____
10	10 HRFM	10-hour fuel moisture	(pct)	____	____	____
11	100 HRFM	100-hour fuel moisture	(pct)	____	____	____
12	1000 HRFM	1000-hour fuel moisture	(pct)	____	____	____
13	X1000 HRFM	X1000 fuel moisture	(pct)	____	____	____
14	WOOD FM	Live woody fuel moisture	(pct)	____	____	____
15	HERB FM	Live herbaceous fuel moisture	(pct)	____	____	____

[1]If a 10 H moisture is input, that same value will be output, except that it will never be less than 2. If the 10 H moisture is entered as 2, a calculated value will appear in the output list.
[2]If man-caused risk is 0, man-caused occurrence index will not be output.
[3]If the lightning risk scaling factor is 0, lightning risk and lightning occurrence index will not be output.
If both man-caused risk and lightning risk scaling factor are zero, man-caused occurrence index, lightning risk, and lightning occurrence index will not be output.
[4]Updatable items not requested because UPDATE is set to **Yes**.

APPENDIX B: (Con.)

SAMPLE NFDR DIRECT OPTION DATA FORM

Name ______________________ Date ____________ Sheet ______ of ______

INPUTS

Line Number	Mnemonic	Item	Range	Value		
1	FUEL MODEL	Fuel model name	(A-Z)			
2	1 HRFM	1-hour fuel moisture	(2-50%)			
3	10 HRFM	10-hour fuel moisture	(2-50%)			
4	100 HRFM	100-hour fuel moisture	(2-50%)			
5	1000 HRFM	1000-hour fuel moisture	(2-50%)			
6	WOOD FM	Live woody fuel moisture	(30-200%)			
7	HERB FM	Live herbaceous fuel moisture	(2-250%)			
8	WINDSPEED	20-foot windspeed	(0-60 mi/h)			
9	SLOPE CLASS	Slope class	(1-5)			
10	STATE WTHR	State of weather	(0-9)			
11	TEMP	Temperature	(0-120°F)			
12	MAN RISK	[1]Man-caused risk	(0-100)			
13	LRSF	[2]Lightning risk scaling factor	(0-1)			
14	Y-LGT OCC	Yesterday's lightning occurrence	(0-100)			
15	LGT ACT LVL	Lightning activity level	(1-6)			

OUTPUTS

Line Number	Indexes and Components		Value		
1	SC	Spread Component			
2	ERC	Energy Release Component			
3	BI	Burning Index			
4	IC	Ignition Component			
5	MCOI	[1]Man-Caused Occurrence Index			
6	LRISK	[2]Lightning Risk			
7	LOI	[2]Lightning Occurrence Index			
8	FLI	Fire Load Index			

[1]If man-caused risk is 0, man-caused occurrence index will not be output.
[2]If the lightning risk scaling factor is 0, lightning risk and lightning occurrence index will not be output.
If both man-caused risk and lightning risk scaling factor are zero, man-caused occurrence index, lightning risk, and lightning occurrence index will not be output.

APPENDIX C: NFDR FUEL MODEL DESCRIPTIONS

The descriptions of the 20 NFDR fuel models are given in the following tabulation:

Model	Loads (T/A) 1 HR	10 HR	100 HR	1000 HR	Herb	Wood	S/V (ft^2/ft^3) 1 HR	Herb	Wood	Heat Content (*Btu/lb*)	Mois Ext (*%*)	Depth (*ft*)	Wind Factor	SCM	Herb type
A	0.20	0.00	0.00	0.00	0.30	0.00	3,000	3,000	1,200	8,000	15	0.80	0.6	301	A
B	3.50	4.00	.50	.00	.00	11.50	700	1,200	1,250	9,500	15	4.50	.5	58	—
C	.40	1.00	.00	.00	.80	.50	2,000	2,500	1,500	8,000	20	.75	.4	32	P
D	2.00	1.00	.00	.00	.75	3.00	1,250	1,500	1,500	9,000	30	2.00	.4	68	P
E	1.50	.50	.25	.00	.50	.50	2,000	2,000	1,500	8,000	25	.40	.4	25	P
F	2.50	2.00	1.50	.00	.00	9.00	700	1,200	1,250	9,500	15	4.50	.5	24	—
G	2.50	2.00	5.00	12.00	.50	.50	2,000	2,000	1,500	8,000	25	1.00	.4	30	P
H	1.50	1.00	2.00	2.00	.50	.50	2,000	2,000	1,500	8,000	20	.30	.4	8	P
I	12.00	12.00	10.00	12.00	.00	.00	1,500	1,200	1,200	8,000	25	2.00	.5	65	—
J	7.00	7.00	6.00	5.50	.00	.00	1,500	1,200	1,200	8,000	25	1.30	.5	44	—
K	2.50	2.50	2.00	2.50	.00	.00	1,500	1,200	1,200	8,000	25	.60	.5	23	—
L	.25	.00	.00	.00	.50	.00	2,000	2,000	1,200	8,000	15	1.00	.6	178	P
N	1.50	1.50	.00	.00	.00	2.00	1,600	1,200	1,500	8,700	25	3.00	.6	167	—
O	2.00	3.00	3.00	2.00	.00	7.00	1,500	1,500	1,500	9,000	30	4.00	.5	99	—
P	1.00	1.00	.50	.00	.50	.50	1,750	2,000	1,500	8,000	30	.40	.4	14	P
Q	2.00	2.50	2.00	1.00	.50	4.00	1,500	1,500	1,200	8,000	25	3.00	.4	59	P
R	.50	.50	.50	.00	.50	.50	1,500	2,000	1,500	8,000	25	.25	.4	6	P
S	.50	.50	.50	.50	.50	.50	1,500	1,500	1,200	8,000	25	.40	.6	17	P
T	1.00	.50	.00	.00	.50	2.50	2,500	2,000	1,500	8,000	15	1.25	.6	96	P
U	1.50	1.50	1.00	.00	.50	.50	1,750	2,000	1,500	8,000	20	1.50	.4	16	P

'A — Annual, P = Perennial.

The surface-area-to-volume ratios (S/V) for the 10-, 100-, and 1,000-H fuels are 109, 30, and 8, respectively. These values are not included as part of the model inputs because they are automatically assigned within the program. Neither do they need to be entered for user models. It is assumed that **all** models will have a 1-HR load and S/V ratio.

Mois Ext is the dead fuel moisture of extinction, in percent.

Fuel bed depth is indicated in feet.

Wind Factor is the adjustment factor by which the 20 mi/h windspeed is multiplied to get the midflame windspeed.

SCM is the maximum probable spread component. It is automatically calculated for and stored with any user model you save.

A/P indicates whether the model is annual or perennial. Because this condition is set for the NFDR models, it can be changed only by getting an NFDR model, changing herb type (input 8) and saving the model as a user model.

Burgan, Robert E.; Susott, Ronald A. Fire danger computations with the Hewlett-Packard HP-71B calculator. General Technical Report INT-199. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986. 16 p.

Describes how to compute indexes and components for the 1978 National Fire-Danger Rating System using the Hewlett-Packard 71B handheld calculator and custom memory. Predicting fire behavior with the HP-71B is described in a separate publication, "Fire Behavior Computations with the Hewlett-Packard HP-71B Calculator," by Ronald A. Susott and Robert E. Burgan, to be issued at a later date.

KEYWORDS: fire danger computations, National Fire-Danger Rating System, portable calculation aid

INTERMOUNTAIN RESEARCH STATION

The Intermountain Research Station provides scientific knowledge and technology to improve management, protection, and use of the forests and rangelands of the Intermountain West. Research is designed to meet the needs of National Forest managers, Federal and State agencies, industry, academic institutions, public and private organizations, and individuals. Results of research are made available through publications, symposia, workshops, training sessions, and personal contacts.

The Intermountain Research Station territory includes Montana, Idaho, Utah, Nevada, and western Wyoming. Eighty-five percent of the lands in the Station area, about 231 million acres, are classified as forest or rangeland. They include grasslands, deserts, shrublands, alpine areas, and forests. They provide fiber for forest industries, minerals and fossil fuels for energy and industrial development, water for domestic and industrial consumption, forage for livestock and wildlife, and recreation opportunities for millions of visitors.

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United States
Department of
Agriculture

Forest Service

**Intermountain
Research Station
Ogden, UT 84401**

General Technical
Report INT-200

March 1986

Proceedings—Symposium on the Biology of *Artemisia* and *Chrysothamnus*

Provo, Utah, July 9-13, 1984

Proceedings of the Third Annual Wildland Shrub Symposium

Sponsored by the Shrub Research Consortium

Institution	Representative
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Brigham Young University Provo, Utah	Dr. Howard C. Stutz
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Proceedings—Symposium on the Biology of *Artemisia* and *Chrysothamnus*

Provo, Utah, July 9-13, 1984

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Symposium Host:

Brigham Young University, Provo, Utah

Publisher:

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Forest Service
U.S. Department of Agriculture
Ogden, Utah 84401

CONTENTS

SYMPOSIUM WELCOME

Bruce N. Smith
Dean, College of Biology and Agriculture
Brigham Young University

On behalf of Brigham Young University, the Shrub Sciences Laboratory of the Intermountain Research Station (USDA Forest Service), and the Shrub Research Consortium, I bid you welcome to this symposium.

I invite you to visit any of the university laboratories, greenhouses, gardens, or libraries. The herbarium is located in the M. L. Bean Museum, which you are most welcome to visit.

The Shrub Sciences Laboratory will also welcome visitors, I am sure. Many people representing diverse interests and a variety of organizations are met together here. We expect an exciting symposium.

As those who went on the field trip are aware, we are pleased to be located in shrub heaven. *Artemisia* and *Chrysothamnus* really like it here so this should be a good setting in which to discuss them.

Part of our commitment to the Shrub Consortium is our intent to establish at Brigham Young University a center of excellence in shrub research. We have on our faculty several people working on aspects of wildland shrubs. A key to our future is the Shrub Sciences Laboratory of the Intermountain Research Station of the USDA Forest Service. A long-term cooperative agreement between the Forest Service and BYU has placed the facility on our campus and made the Shrub Lab professionals adjunct faculty members at BYU. Durant McArthur, our able program chairman, is a good example of the caliber of people involved.

As you will see in these proceedings, the work has barely begun. There is much to be done. We need active cooperation with scientists from around the world. We must coordinate our research efforts. In that spirit we welcome you most heartily to this conference. May your week be a most profitable one.

INTRODUCTION: ARTEMISIA AND CHRYSOTHAMNUS

E. Durant McArthur and Bruce L. Welch

These proceedings are the third in a series on the biology and management of western wildland shrubs. Earlier accounts provide information on bitterbrush (Purshia), cliffrose (Cowania), and related rosaceous species and on Atriplex and related chenopods (Tiedemann and Johnson 1983; Tiedemann and others 1984). Proceedings of the fourth symposium are in preparation. That symposium dealt with plant/animal interactions with an emphasis on woody plants and mammalian herbivores. All four proceedings have been or will be published by the Intermountain Research Station. Various institutions have cosponsored the symposia. The Shrub Research Consortium (see the inside front cover of these proceedings) now has the continuing role of sponsoring periodic symposia and workshops on shrub biology and management.

These proceedings include contributions in the general areas of distribution, systematics, and genetics; revegetation and plant control; animal relationships; ecological relationships; entomology and pathology; and physiology for the genera Artemisia and Chrysothamnus. The genera Artemisia and Chrysothamnus provide interesting contrasts and parallels. Both are members of the family Asteraceae (Compositae) and both are important members of the vast shrublands of the Intermountain West (Küchler 1964; McArthur 1984). The 54 papers in these proceedings substantially review and expand the knowledge base for these two genera. Modern interest in their taxonomy and management owes its foundation to the seminal work of Hall and Clements, especially as embodied by their treatise of 1923 (Hall and Clements 1923).

Artemisia (wormwood, southernwood, tarragon, mugwort, wormseed, sagebrush, and others) is a widespread, mainly temperate and northern genus (Grieve 1931; Good 1974; McArthur 1984). Artemisia belongs to the tribe Anthemideae (Heywood and Humphries 1977). It is composed of some 400 species divided into four subgenera (Artemisia, Dracunculus, Seriphidium, and Tridentatae) based mostly on floral, but also on chemical and distributional characteristics. Although some other Artemisia species are important--for example, sandsage (A. filifolia), budsage (A. spinescens), fringed sage (A. frigida), Louisiana sagewort (A. ludoviciana), tarragon (A. dracunculus), and California sage (A. californicia)-- big sagebrush (A. tridentata) and its close relatives (subgenus Tridentatae) are the Artemisia landscape dominants of western North America (McArthur and Plummer 1978; McArthur 1984). Tridentatae includes approximately 20 taxa (McArthur and others 1981; Shultz these proceedings). In addition to the biological and management information presented in these proceedings we recommend consulting these publications for entry into the literature and further information:

Hall and Clements 1923
Plummer and others 1955, 1968
Beetle 1960
Johnson 1977, 1979, 1983
Plummer 1977
McArthur and Plummer 1978
McArthur and others 1979
Utah State University 1979
Welch and McArthur 1979
Winward 1980
Harniss and others 1981
Tisdale and Hironaka 1981
Blaisdell and others 1982
Johnson and Fisser 1984

Chrysothamnus (rabbitbrush) is a genus of some 20 shrub species endemic to western North America. Chrysothamnus belongs to the tribe Astereae (Anderson 1970; McArthur and others 1978). It is similar to subgenus Tridentatae, the sagebrushes, in that both groups occupy the same general geographic area. Often species of both groups are to be found in the same plant communities. Both groups of plants also share the characteristic that some of their members are considered useful forage by range managers and other members are sometimes the object of eradication to improve quality of range livestock forage (Hall and Clements 1923; Hanks and others 1975; Keller 1979; McArthur and others 1979; and papers in these proceedings). Both genera are characterized by plants with a rich array of secondary metabolites (Herz 1977; Heywood and others 1977; Heywood and Humphries 1977). The classes of these metabolites in the two groups are quite different. For example, Artemisia is rich in sesquiterpene lactones and Chrysothamnus (C. nauseosus) is rich in rubber. They differ in distribution. Artemisia has a wide extra-North American distribution, Chrysothamnus is restricted to western North America.

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Both genera have species that dominate landscapes but that characteristic is much more common in Artemisia. Often landscapes dominated by Chrysothamnus species have been disturbed. Some Chrysothamnus species are rapid invaders of disturbed plant communities. Both sagebrush (Tridentatae) and rabbitbrush include large species complexes that tend to overshadow other members of their respective groups. For sagebrush, the most important species complex is big sagebrush (A. tridentata); that role is assumed by rubber rabbitbrush (C. nauseosus) in rabbitbrush.

More and more, subspecific taxonomic designations are used for these and other species complexes in the two groups (Tridentatae, Chrysothamnus). We support this trend and believe and hope that it will continue. Nevertheless, taxonomic determinations are not always easy, even for experts. We believe both groups have clusters of taxa that are actively speciating and that some intermediate forms are difficult to pidgeonhole taxonomically.

For information in addition to that presented in these proceedings on the taxonomy and management of Chrysothamnus and for entry into the literature we recommend that the following references be consulted:

Hall 1919
Hall and Clements 1923
Anderson 1966, 1970
Plummer and others 1968
Hanks and others 1975
Plummer 1977
McArthur and others 1978, 1979

ACKNOWLEDGMENTS

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Section 1. Field Trip

FIELD TOUR--THE BIOLOGY OF ARTEMISIA AND CHRYSOTHAMNUS

Alma H. Winward and Loran C. Anderson

In conjunction with the wildland shrub symposium, "The Biology of Artemisia and Chrysothamnus," a 2-day field tour was conducted in central Utah. This tour was designed to allow interested participants an opportunity to see several of the sagebrush (Artemisia) and rabbitbrush (Chrysothamnus) taxa in their natural settings. We attempted to describe important taxonomic and ecological characteristics associated with each taxon of these two genera at each stop.

The field trip began July 9, 1984, at Provo, UT. We traveled southward through the central Utah communities of Springville and Huntington to Richfield (overnight), then northward through Fillmore, Nephi, and back to Provo with various stops between at selected populations of sagebrush and rabbitbrush. We were able to observe over 20 species and subspecies of these two important western genera.

MONDAY - JULY 9, 1984

Stop #1. Springville Nursery

At this first stop we observed several accessions of big sagebrush species and subspecies growing in a common garden. The garden is maintained through a cooperative effort between the U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Shrub Sciences Laboratory, and the Utah Division of Wildlife Resources. We also were able to observe results of selective use by mule deer that were allowed into the garden area the preceding winter and spring.

Stop #2. Thistle Slide Area

This was a general-interest stop to allow participants an opportunity to view effects of the massive slide. This slide deposited millions of tons of earth into the Spanish Fork Canyon forming the temporary Thistle Lake. The group was able to observe the awesome scenes remaining after the lake was lowered.

Stop #3. Milburn Junction

We stopped just east of Highway 89 on the road to Milburn at an Artemisia tridentata ssp. tridentata site. Not many acres of ssp. tridentata remain in this portion of the State since most have been put into agricultural production. Subspecies tridentata grows on deep, well-drained soils and, aside from a few special accessions, is generally more valuable for its cover values than foraging aspects. Since this subspecies can be confused with other big sagebrush subspecies, we took time to demonstrate useful characteristics used to differentiate it. The persistent leaves are long and narrow compared to the shorter and belled lobes of ssp. wyomingensis. Also ssp. wyomingensis generally has deep-lobed ephemeral leaves. Subspecies tridentata is differentiated from ssp. vaseyana based on shrub shape and the relative length of the vegetative versus the flower stalks. Subspecies tridentata has vegetative stalks more than half as long as the adjacent flower stalk while ssp. vaseyana has vegetative stalks less than half the length of the nearest flower stalk. Subspecies vaseyana also fluoresces a bright creamish-blue color under long-wave ultraviolet light when soaked in water or alcohol. The other two subspecies have no or very little fluorescence.

Several kinds of rabbitbrush were seen at this site. Mountain low rabbitbrush (C. nauseosus ssp. lanceolatus) was frequent among the sagebrush. Two subspecies of C. nauseosus were present: ssp. consimilis and ssp. hololeucus. Although they have different "preferred" ecological sites, they obviously can grow together. Threadleaf rubber rabbitbrush (ssp. consimilis) has generally narrower leaves than ssp. hololeucus and usually occurs in somewhat saline soils. Subspecies hololeucus grows in better drained soils of the Great Basin and in the mountains of central Utah. It is often confused with ssp. albicaulis which grows more in Idaho and the Pacific Coast States. Both of these taxa have hairy white stems (tomentose) but differ in floral characteristics. Other rabbitbrushes seen here were C. vaseyi (near the northern limit of its range) and C. parry ssp. attenuatus.

This paper is an invited account of the July 9-10 field trip conducted during the symposium, Biology of Artemisia and Chrysothamnus, Provo, UT, July 9-13, 1984. It is adapted for do-it-yourself visits.

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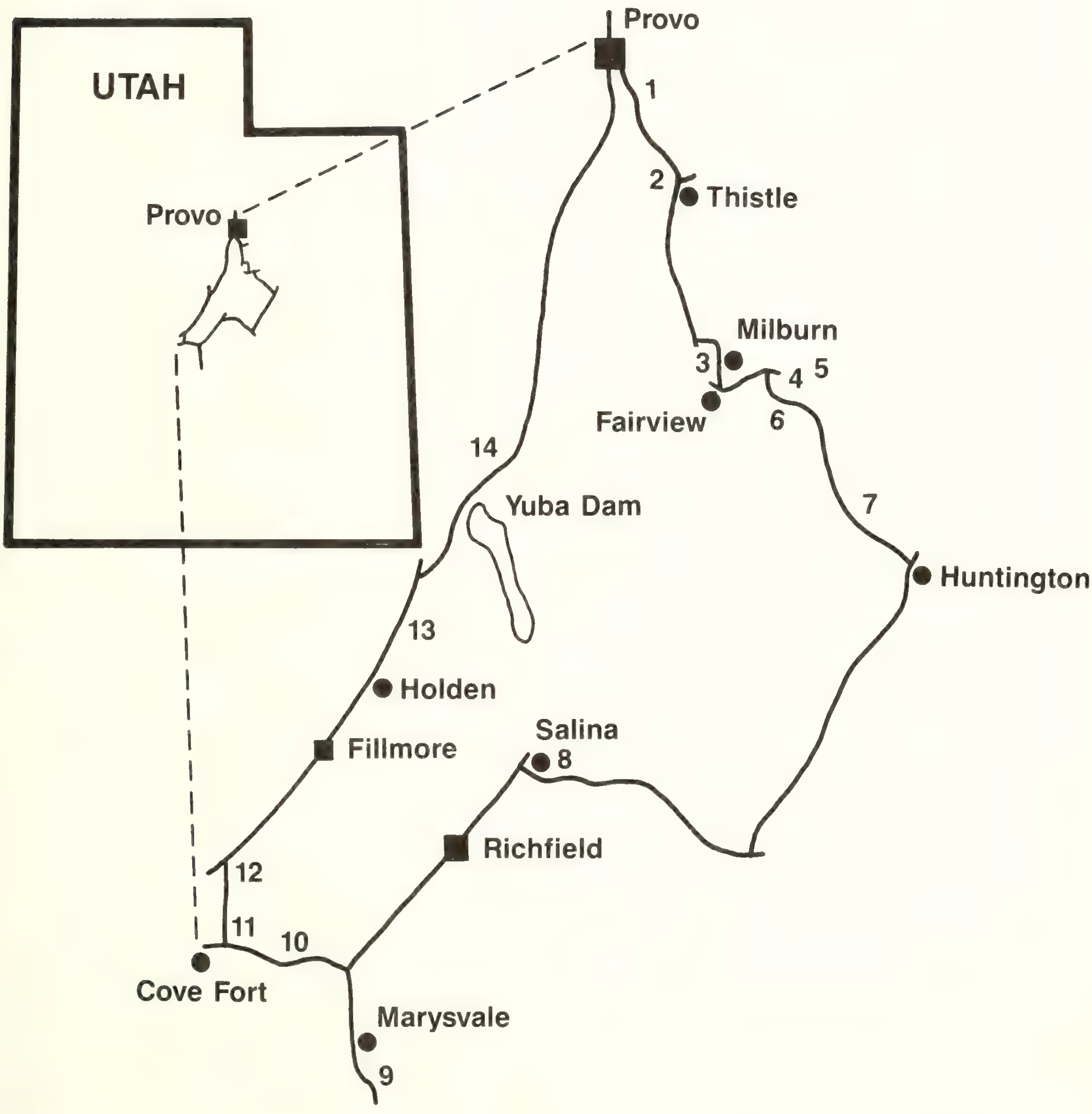
FIELD TOUR
BIOLOGY OF ARTEMISIA AND CHRYSOTHAMNUS

Stops 1-8, July 9, 1984
Stops 9-14, July 10, 1984



Stop #4. Fairview Canyon Summit (1)

Vegetation at this stop was dominated by A. tridentata ssp. vaseyana. This subspecies is common in the mountainous areas of most western States. It is found on well-drained, moderately deep soils, as is ssp. tridentata, but is restricted to the cooler, more moist mountain climates. This particular stand demonstrated the flat-topped growth form common in ssp. vaseyana. We pointed out the diversity of associated species and general high production capabilities of this site. We also discussed potential high cover and density values often found associated with poor condition vaseyana sites. Unlike ssp. tridentata and wyomingensis, ssp. vaseyana seeds stored in the surface soils tend to be stimulated by fire. We discussed implications of this for management of these sites.

At this site, C. viscidiflorus ssp. lanceolatus is diploid (2n = 18); those seen at Stop #3 were tetraploid (2n = 36). Chromosomal races of this subspecies are generally separated altitudinally.

A mountain form of C. nauseosus (ssp. salicifolius) is found only in northern Utah and occurs sporadically here on the Wasatch Plateau. At our lunch stop just below Fairview Summit, we saw a specimen of this wide-leaved taxon (salicifolius means willow-leaved). The plant was not yet in full bloom; most C. nauseosus bloom a few to several weeks later than C. viscidiflorus when they occur together.

Stop #5. Fairview Canyon Summit (2)

Closely associated with Stop #4 were stringers or islands of A. cana ssp. viscidula. This subspecies is adapted to areas where moisture in the soil profile persists into the summer months. During spring these sites may be super saturated or even flooded. Subspecies viscidula is able to persist in these seasonally wet situations while subspecies of A. tridentata would drown out. Subspecies viscidula sites support a high diversity of grass and forb species and often produce 1,780 lb/ac (2 000+ kg/ha) of dry weight vegetation. We discussed the importance of separating ephemeral from persistent leaves on this taxon since ephemerals may or may not be lobed while persistent leaves are nonlobed. We also observed here the herbaceous A. ludoviciana ssp. incompta which is a common plant at higher elevations of the Wasatch Plateau.

Stop #6.

At the highest point of our tour, approaching 9,000-feet (2 743-m) elevation, we encountered two unique sagebrush taxa. One has characteristics similar to ssp. vaseyana encountered at Stop #4 except for larger seed heads with six or more seeds per head. Previously this taxon has been referred to as A. tridentata ssp. vaseyana forma spiciformis. However, workers at the Shrub Sciences Laboratory recently have determined from the type specimen collected in Washington State that this taxon is the originally named "vaseyana". There is a proposal to name this ssp. vaseyana var. vaseyana, and the variant described at Stop #4 as ssp. vaseyana var. pauciflorus (meaning few flowered). This effort would keep both variations as vaseyana with distinction available at the variety level since they do have genetic and environmental differences.

The other type of sagebrush at this stop is common at higher elevations in northeastern Utah, southeastern Idaho, southwestern Wyoming, and northwestern Colorado. It has large seed heads with more than six flowers per head, has large, sharp-pointed and deeply divided leaves, and has the unique distinction of being the only member of the A. tridentata group that is able to resprout. It has been erroneously referred to as A. rothrockii or A. cana. The type specimen of this variant is from Colorado and has been named "spiciformis." This taxon is in the process of being named A. tridentata ssp. spiciformis. It is differentiated from other tridentata taxa by its resprouting characteristic and several morphological differences that will be described in a forthcoming article from the Intermountain Research Station. It can be best separated from A. rothrockii, a Sierran species, by geographic distribution as well as such morphological features as shrub height and leaf pubescence.

Stop #7.

As we proceeded down Huntington Canyon, we stopped at approximately the 5,700 foot (1 737-m) level and observed several additional Artemisia and Chrysothamnus taxa. Artemisia nova, a low-growing, often bright green leaved shrub is well adapted to this relatively droughty site. It is known from most western States and occurs in two color phases: green, as found here, and gray. The green color phase is readily separated from other sagebrush by color, stickiness, and smell. The gray phase is more difficult to differentiate, especially from A. arbuscula. Stickiness of crushed leaves and smell help, but often a hand lens observation of leaf pubescence is required. Artemisia nova has obvious resin glands visible on leaf surfaces and a matted, tangled, or mashed type of pubescence, while A. arbuscula has glands almost camouflaged by a soft, singular, fluffy pubescence. Also A. arbuscula often can be separated by its bright bluish fluorescence in alcohol or water.

We also observed plants of A. bigelovii at this stop. This species has a more southern distribution and is common in the southwestern States. It is one of our most drought-resistant sagebrushes. It is most easily separated from other sagebrush taxa in the Great Basin by presence of a few ray flowers. With experience, it may also be distinguished by presence of relatively sharp-pointed leaf lobes and its low, many branched growth form.

Two relatively large rabbitbrushes were found in the wetter sites along the highway. Flax-leaved or spreading rabbitbrush (C. linifolius) has broad, smooth dark green leaves and is the only species in the genus that regularly forms large colonies by underground rootstocks (soboliferous). Some specimens of this species seen in southern Utah were 12-feet (3.7-m) tall. Green rubber rabbitbrush (C. nauseosus ssp. graveolens) looks much like ssp. consimilis seen at Stop #3 but is somewhat more robust, has wider leaves, and occurs generally more to the east of ssp. consimilis (central Utah to Colorado and the Dakotas).

A third low-growing rabbitbrush was on the drier, rocky slopes with A. nova; this was C. viscidiflorus ssp. puberulus. Abundant short, fine hairs give a dull cast to its foliage. Its major range is the Great Basin, and this site is near the eastern limit of the subspecies.

Stop #8.

Our last stop of the day was at the mouth of the canyon just east of Salina. Here we observed differential insect preference for two subspecies of Chrysothamnus nauseosus. Gall forms on ssp. consimilis can be described as cottony, whereas those on ssp. hololeucus are smooth and hard--the callus form.

TUESDAY - JULY 10, 1984

Stop #9. Marysvale/Piute Area

As we proceeded south out of Richfield, beyond the Big Rock Candy Mountain we encountered extensive "flats" of A. tridentata ssp. wyomingensis. This is the most drought-resistant member of A. tridentata and occurs on sites that sharply contrast those of A. tridentata ssp. spiciformis and other big sagebrush taxa observed the first day. Precipitation here is 8-11 inches (20-28 cm) annually with long, hot summer periods. Potential biomass is normally 400-800 lb/ac (448-896 kg/ha) at best and, on this site, was mostly in sagebrush. Most understory species have been lost as a result of past management activities. Subspecies wyomingensis sites have natural low diversity of associated species and are difficult to revegetate with herbaceous species except for Agropyron cristatum or similar drought-resistant grasses. We discussed the problems associated with restoring these sites due to their droughty nature and the availability of seed from native species and/or adaptability of introduced species. We presently have many acres of ssp. wyomingensis in a similar poor ecological condition and with low species diversity. We reinforced our taxonomic separation of this subspecies from others seen the first day (see Stop #3).

The frequently seen C. nauseosus ssp. hololeucus (white rubber rabbitbrush) was found along the edge of the ssp. wyomingensis flats, and C. greenei was found sporadically in the flats. Chrysothamnus greenei looks much like C. viscidiflorus but has pointed involucral bracts in the flower heads; it often occurs in nearly pure stands with Ceratoides (Eurotia) lanata in the basins of western Utah and adjacent Nevada.

Stop #10. Clear Creek Pass

At the top of Clear Creek Pass, enroute to the Cove Fort area, we stopped to collect samples of A. tridentata ssp. vaseyana ("pauciflorus") for comparison with sagebrush at the next stop (Stop #11). Here, too, we observed Artemisia dracunculus, an herbaceous species with long, narrow, entire, bright green leaves. This is the tarragon of the herbalist. We also observed several subspecies of Chrysothamnus, particularly C. parryi ssp. attenuatus and C. viscidiflorus ssp. viscidiflorus.

Stop #11. Cove Fort (1)

As we descended into the valley surrounding Cove Fort, we stopped to observe the large stands of sagebrush and rabbitbrush along the bench areas. An initial glance at the sagebrush and the ecological setting indicated a ssp. wyomingensis site. However, closer observations showed this to be a unique variation of ssp. vaseyana. We have encountered this variant in several locations in Nevada, Utah, and southern Idaho. It occurs at or just below the pinyon/juniper belt. It often has a cuneate, bell-shaped leaf like ssp. wyomingensis but has slightly longer flowering stalks and fluoresces bluish under alcohol and water as does ssp. vaseyana. At its upper range it blends into ssp. vaseyana at about the oakbrush zone. Although it is not yet a recognized separate taxon, it is important that land managers separate it from ssp. wyomingensis. Unlike ssp. wyomingensis, sites supporting this variant have higher potential for natural diversity and management opportunities. Seedings may include bitterbrush (Purshia tridentata), alfalfa (Medicago sativa), Lewis flax (Linum lewisii), intermediate wheatgrass (Agropyron tricophorum), and other species suited to ssp. vaseyana but not ssp. wyomingensis sites.

We took time to fluoresce a few leaves of this sagebrush to demonstrate its close relationship to ssp. vaseyana.

Two subspecies of C. viscidiflorus grow together here. The smaller plants of ssp. puberulus were abundant, and the larger, greener plants of ssp. viscidiflorus were more restricted on the slightly more favorable sites (depressions with more moisture and deeper soils). Low-growing forms of ssp. viscidiflorus have been called ssp. pumilus, and very narrow-leaved forms have been called ssp. stenophyllus. Experimental studies have shown that both are just environmental variants and should not be separated from ssp. viscidiflorus. We saw C. vaseyi again; it looks somewhat like C. viscidiflorus but is easily distinguished

because it lacks hairs on the seeds that characterize most other rabbitbrush taxa we have seen on the tour.

Horsebrush (Tetradymia canescens) was examined also; it is sometimes confused with C. nauseosus, but Tetradymia has only four bracts in the flower heads rather than several in layers as in rabbitbrushes.

Stop #12. Cove Fort (2)

Approximately 1 mile north of Cove Fort we stopped to again observe the droughty variant of ssp. vaseyana just seen at Stop #11. We dug a soil pit to get a feeling for its site relationships compared to other big sagebrush taxa.

Stop #13.

After lunch at Fillmore, we traveled to an area just north of Holden administered by the Utah Division of Wildlife Resources. Here we observed a successful planting of pubescent wheatgrass onto a site previously occupied by the droughty vaseyana observed around Cove Fort. We also were able to see interplantings of sagebrush, rabbitbrush (mostly ssp. hololeucus), and other shrubby species established into the pubescent wheatgrass for wildlife forage and diversity.

Stop #14.

Our final stop of the tour was just northeast of the dam on Yuba Lake. Here we observed islands of A. nova on appropriate sites and a few small stands of A. pygmaea. Artemisia pygmaea is a dark green cushionlike shrub easily identified from other sagebrush by its pinnatified leaves (3-11 lobes). Thus far, this species is found only in the States of Utah, Nevada, and Arizona. It occurs on special sites believed to be strongly calcareous. More needs to be known about this species since it appears limited to a few special sites.

On the drier, rocky sites with A. pygmaea, we observed what looked like a somewhat "anemic" C. nauseosus ssp. consimilis. It was ssp. leiospermus which is distinguished from ssp. consimilis in having glabrous seeds (no hairs below the pappus hairs on the end of the seed). We saw yet another subspecies of C. nauseosus (ssp. turbinatus) beside the road. Unfortunately there wasn't much of it, and it was heavily galled which made characterization difficult. It prefers sandier sites in southwestern Utah but also occurs sporadically east of the Wasatch Plateau.

We returned to Provo at approximately 5:00 p.m. via Nephi.

SPECIES AND SUBSPECIES OBSERVED ON THE FIELD TOUR TO ARTEMISIA AND CHRYSOTHAMNUS SITES IN CENTRAL UTAH

ARTEMISIA (SAGEBRUSH)

A. bigelovii (Bigelow sagebrush)
A. cana
    ssp. viscidula (mountain silver sagebrush)
A. dracunculus (tarragon)
A. ludoviciana
    ssp. incompta (mountain Louisiana sagewort)
A. nova (black sagebrush)
A. pygmaea (pygmy sagebrush)
A. tridentata
    ssp. tridentata (basin big sagebrush)
    ssp. vaseyana (mountain big sagebrush)
    ssp. wyomingensis (Wyoming big sagebrush)
    ssp. spiciformis (subalpine big sagebrush)

CHRYSOTHAMNUS (RABBITBRUSH)

C. linifolius (spreading rabbitbrush)
C. nauseosus
    ssp. consimilis (threadleaf rubber rabbitbrush)
    ssp. graveolens (green rubber rabbitbrush)
    ssp. hololeucus (white rubber rabbitbrush)
    ssp. leiospermus (smoothseed rubber rabbitbrush)
    ssp. salicifolius (mountain rubber rabbitbrush)
    ssp. turbinatus (sand rubber rabbitbrush)
C. parryi
    ssp. attenuatus (thinleaf Parry rabbitbrush)
C. vaseyi (Vasey rabbitbrush)
C. viscidiflorus
    ssp. lanceolatus (mountain low rabbitbrush)
    ssp. puberulus (hairy low rabbitbrush)
    ssp. viscidiflorus (stickyleaf low rabbitbrush)

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UTAH GEOLOGY AND BOTANY

Stanley L. Welsh

ABSTRACT: This paper is a result of an invited lecture on the field trip of the Biology of Artemisia and Chrysothamnus symposium. In it Dr. Welsh traces his beginnings as a geobotanist to an assignment at Dinosaur National Monument. Some relationships between plant distributions and geology in Utah are described.

The view at my front was one of awe and splendor. Parallel ridges of varicolored rock extended east along the southern flank of the Split Mountain anticline in Dinosaur National Monument. Steeply plunging rock formed hogbacks and cuestas. Between the ridges, minor drainages occurred along the strike of the formations, paralleling the strata awhile before plunging at right-angles through the tilted, more resistant layers of rock. The backdrop of Split Mountain stood as a grand phenomenon, with the Green River flowing through, instead of around, the anticline.

This was my introduction as a practical field botanist to the technicolor geology of eastern Utah. Before my eyes was a whole new world, one where the aridity of the land produced a naked or nearly naked landscape. Its geology could be viewed without hindrance of an obscuring mantle of vegetation. Yet, vegetation was present in the picture. Portions of the geological setting were obscured, but not enough to prevent even a novice from detecting the differences in strata, their color, texture, and composition. Salts coated the margins of seeps and the few tiny streams flowing across the formations in the vicinity indicating the presence of water-soluble materials. The salts had not been leached away by water and now appeared like eternal snow. But the landscape, carved as it was into a badlands topography, gave evidence of the action of water as a principal erosive element.

Geomorphological features within my view had been carved by the combined effects of water, wind, heat, and cooling. The water had not been placed gently on the land, but came, as it still does, in feast-or-famine amounts. When the rains come, the water strikes the naked or nearly naked slopes, the surface is soon saturated, and then the water runs overland, cutting the substrate and carrying it away down the great river system of the Green-Colorado. Rills become gullies and these become canyons downward along the headcutting system. The water reads the underlying substrata and follows the paths of least resistance. The shape of sequential and resequential tributaries thus formed is controlled by the hardness of the rocks. Wind and alternating heat and cold serve to pry loose fragments of stone and alluvium from previous erosive cycles; water then adjusts them into the most stable contours possible. No particle of material is allowed to remain constantly free. Even the most resistant stone is removed grain by grain and redeposited again, usually following a series of moves, into other stone at some other place.

The scene east of the Dinosaur Quarry was marked by sandstone ridges alternating with softer mudstone or siltstone and shale valleys. The summits of the parallel ridges were approximately the same elevation, about a mile above sea level in the vicinity of the quarry, but increased gradually up the slope of the anticline toward the heights of Split Mountain. Even in the lower reaches, where one would expect the amount of precipitation to be approximately equal from year to year, and where vegetation should reflect that amount with some degree of uniformity, the plants from stratum to stratum were not the same. The vegetative cover, thin though it was, reflected the underlying geology. Each of fourteen formations, from Mancos Shale to Weber Sandstone (Cretaceous to Pennsylvanian), supported vegetation that differed in subtle ways from that on adjacent formations. The salt-desert shrub and annual-dominated plant communities of the Mancos Shale gave way abruptly at the margin of the Frontier Formation, with its widely spaced juniper and Utah serviceberry. That thin covering of shrub species changed again at the margin of the acidic Mowry Shale, which is marked with parallel rows of Eriogonum corymbosum and E. lonchophyllum var. saurinum. The basic Morrison, Carmel, and Moenkopi supported clumps of a milkvetch of great beauty, Astragalus saurinus, an endemic to those and similar formations in the immediate area. Growing on the Entrada Formation was the newly described grass milkvetch, Astragalus chloodes, another narrow endemic of sandstones of the Uinta Basin.

On each of the formations, the basic community type changed abruptly where the alluvium obscured the underlying geology, insulating the vegetation from the peculiarities of the individual formations. The plants were displaying the different chemical and physical makeup of the formations and of the alluvium derived from them.

Thus began my association with geology and botany. The appellation "geobotanist" has been applied to me, especially by my Russian colleagues.

Research dealing with the ecology of higher plants of Dinosaur National Monument involved learning the stratigraphy of the region. Fortunately for me there

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were in Vernal, UT, two eminently qualified geologists who were more than happy to aid this novice. G. E. (Ernest) and B. R. (Billie) Untermann were in charge of the State museum in Vernal. This remarkable husband-and-wife team had spent their lives in the area learning about its geology, and had in preparation a field guide to the geology of the Uinta Mountains and vicinity (Untermann and Untermann 1954). They gave me a manuscript copy and instructed me in features of geological strata. With that information I went again to Dinosaur, to view the unmatched scenes. Soon my footprints marked each of the formations as I collected plants. The sequence of strata became a part of my memory, and it is to that type series of formations that I compare all geology of the State. A side benefit was, of course, the friendship that grew between the Untermanns and me. Much later, after both had died, I named a species of daisy Erigeron untermannii (Welsh 1983) in honor of that amazing couple. The studies at Dinosaur led to completion of a thesis on the vegetation of Dinosaur National Monument (Welsh 1957).

Following completion of my doctoral degree in 1960, I returned to Utah where I began what has developed into a lifetime of wandering through the geology of the State in search of plants, a study aided by geologists at Brigham Young University, especially by Dr. Keith Rigby and Dr. Lehi Hintze.

Utah is huge and its geology diverse. Classification of the stratigraphy of the State has been under way for a long time. There are hundreds of named formations, with some further divided into members or other subunits (Hintze 1972). To know all of them requires a lifetime of concerted effort, which I have not made. However, there are some natural divisions that make the task of understanding Utah's geology easier. The State is divided into two portions by an overthrust belt that runs from northern to southwestern Utah. West of the eastern margin of that overthrust zone, the geological formations are gray in color, with minor exceptions, and the rocks are old, consisting mainly of limestone and dolomites, but with some major quartzites. They range in age from Precambrian to Pennsylvanian, marked here and there with younger sequences derived mainly from the products of erosion, or by igneous deposits.

The mountain ranges of the Great Basin belong to that western section. These mountains are the bases of still older mountains that arose in Paleozoic times and were worn away in the Mesozoic. The products of erosion were carried to the east where they were deposited in a shallow sea. Mancos Shale is a product of such deposition. The worn mountains were faulted, uplifted, and thrust to new heights in a landlocked basin, and are now hip-deep in their own detritus. The great bajadas and fans of the Great Basin have no counterpart in the Colorado Basin. The Great Basin is a region of accumulation of detritus and alluvium; the Colorado Basin is one of excavation. The difference can be noted easily by discerning the location of aggregate-quarrying operations. Gravel can be taken from lacustrine or fluvial deposits almost anywhere in the valleys of the Great Basin, but in the Colorado Basin the gravels are taken mainly from ridge crests where ancient pedimental deposits are hung between entrenched drainages.

The faulted gray geology of western Utah is interesting mainly to those who are color blind and to those who find challenging the subtle differences in texture and color, or are encoding fossils of that geology. Even where the stratigraphy is subtle, and it is difficult for geologists to detect the differences, some plant species occur with remarkable consistency on strata or portions of strata that appear to be the same to the untrained. Sevy Dolomite is such a formation. It is exposed in western Millard and Beaver counties, and supports a unique vegetation consisting of peculiar buckwheats, catseyes, globe mallow, and cacti.

Many of the strata are buried beneath the accumulated debris of the mountains themselves. Most low-elevation geology involves alluvium and other valley fill. While some of the alluvium approaches the character of the formations from which it is derived, most does not. Changes in particle size and mixing with other parentally derived material dictate differences in water and mineral relations. Vegetation on the bajadas, alluvial fans, and valley floors consists of different community types than that on the mountains proper, where the original strata are exposed to the plants directly. The species might be the same, in large or small part, but the community structure is different.

Comparable elevations in the Colorado Basin do not bear the vast expanses of alluvium, and the vegetation grows directly on the exposed geological strata. The peculiarities of those strata are reflected directly by the plants growing on them. The exposed geological strata of the Colorado Basin result in a large number of habitats not available in western Utah. Plants respond to the habitats available by developing ecotypes that can survive on the peculiar substrates, often without significant competition from other plants. Many low-elevation endemics occur in the Colorado Basin, but the Great Basin does not have endemics in the same proportion at lower elevations, even discounting the preexistence of Lake Bonneville.

In order for the geological substrates to be controlling, in Utah at least, the area must be xeric. Desiccation is apparently a necessity for ultimate expression of edaphic control of vegetation; that desiccation can be actual or physiological. There are areas in the State where fine-textured substrates occur at high elevations. At those elevations, the surface layers of the formations are treated to greater precipitation and leaching of some of the soluble salts. Plants that do grow form a compact vegetative cover. Organic material accumulates and soil formation results. The soil acts to insulate the plants from the parent material. Edaphic control by the parental substrate becomes less important and other features become controlling. Plants that occupy the developed soils tend not to be specialists; they are broadly distributed. Diversity tends to be low.

However, even at high to very high elevations there are xeric sites, despite the occurrence of increased

precipitation. Xeric sites are geomorphologically controlled. Plateau margins, cliff faces, and other steep sites, where water is shed easily and where exposure is such that energy per unit area is high, are examples of xeric sites at high elevations. The substrate there is controlling also, and other peculiar habitats are present. Endemic plant taxa grow on them also. Note the occurrence of Silene petersonii on the margins of the Flagstaff Limestone of the Wasatch Plateau, and the Pink and White Limestone Members of the Wasatch Formation on the Sevier and Paunsagunt plateaus. Other plants with similar distribution include: Astragalus montii, Eriogonum aretioides, Cryptantha ochroleuca, Eriogonum panguicense, Lomatium minimum, Lesquerella rubicundula, Penstemon bracteatus, Townsendia montana, and Cymopterus minimus.

The geologic strata discussed previously are mainly sedimentary. Igneous geology is important over much of the State, however. Both intrusive and extrusive materials are present in such places as Marysvale, where igneous deposits up to 30,000 ft (9 150 m) thick cover a shield-shaped area more than 50 mi (80 km) wide, the laccolithic mountains of the Henry's, La Sal's, and Abajo's, and the basalt flows near Panguitch Lake, Black Rock, and St. George. The igneous deposits are diverse in type, form, texture, and composition. Some of them are further complicated by chemical or thermal modification. Big Rock Candy Mountain, Monroe Hot Springs, and the Tushar Mountains consist at least in part of thermally modified rocks. There are examples of plant species endemic to many of the peculiar igneous substrata. The high-elevation portions of the Tushar Mountains contain half a dozen examples of endemic species including Astragalus perianus, Castilleja parvula, Lesquerella wardii, Draba sobolifera, Gilia tridactyla, Penstemon tusharensis, and Penstemon parvus.

Thus, the search for peculiar plants in Utah is correlated with the location of peculiar geological strata. The fine-textured formations, the limestones, shales, siltstones, and mudstones, which I lump under the inclusive term "garp," contain most of the endemic species. The Moenkopi, Chinle, Carmel, Entrada, Mancos Shale (including Tropic Shale), Uinta, and Duchesne River formations are examples of strata with fine-textured substrates. Each of these supports one or more peculiar species of plant with some special genetic structure.

Walter P. Cottam is reported to have said of the Mancos Shale, where he camped one night, that there were only four plant species growing on the formation and that he didn't know three-fourths of the flora. One should not expect to walk onto Mancos Shale and immediately begin collecting new and undescribed species. Rare plants do not exist in high numbers; neither do they occupy the entire formation. The plants grow as small populations scattered here and there on the stratum, often restricted to some minor subunit or chemically differing portion. Water relations are poor and soluble salts are high. Presence of gypsum and selenium often complicates plant growth. The combination of high salt concentrations (up to 30,000 ppm), gypsum, selenium, colloids, and other substances tends to restrict plants to those species that can tolerate the poor qualities. Those that can grow there are not subjected to much competition from other plant species.

Sandstones and other coarsely textured strata also support peculiar plant species, but the reasons are less obvious. The Cedar Mesa Sandstone, a member of the Cutler Group of formations, bears the distinctive Astragalus monumentalis, but the White Rim Sandstone, a member of that same group but borne stratigraphically above the Cedar Mesa, does not support that species. Rather, on the White Rim there occurs a similar, but wholly distinct taxon, Astragalus desperatus, a generalist on many formations.

Much work remains to be done. The State contains some 84,000 mi^2 (218 000 km^2) of land. Perhaps a quarter of that area is sufficiently well-known botanically and geologically to require little additional study, but we have lifetimes of work left to do.

Those who would understand the flora of any region must view the geological basis carefully. The plants are often better stratigraphers than are the geologists, as sheep are the ultimate botanists. Thus, I recommend that those who study plants should study geology also, and don't forget about the sheep.

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HABITAT TYPE, RANGE SITE, AND COMMUNITY TYPE

M. Hironaka

ABSTRACT: Placement of habitat type, range site, and community type in a hierarchy forms a framework for an ecologically based information storage-retrieval system for land management. The community type classification concept needs to be revised to associate community types to respective habitat types.

CLASSIFICATION BASED ON VEGETATION

Today, three land classification schemes based on vegetation are used by land management agencies. Researchers use these classifications to describe the setting of their study areas and to project applications of their findings to areas of similar capabilities.

Habitat type is the most recent of the classification schemes (Daubenmire 1952). It is an ecological classification and is based on climax vegetation. By definition the habitat type is the aggregate land area that presently supports, or until recently supported, and presumably is again capable of supporting the same climax vegetation (Daubenmire 1968). Thus, the habitat type is the land area that has the same effective environment as is evidenced by its present or recent support of the same climax vegetation. From a mapping viewpoint, all land that supports or supported the same specific climax vegetation is of the same habitat type. Different habitat types occur because the effective environment is different and in turn supports or supported different climax vegetation. From a land management viewpoint, lands within the same habitat type have similar potential because of similar effective environment.

Range site classification was introduced earlier than the habitat type classification by about 3 years. The former was introduced by Dyksterhuis (1949) of the U.S. Department of Agriculture, Soil Conservation Service. Range site classification is an ecological classification based on climax vegetation, also. In addition, it is based on site productivity and/or species composition uniformity due to site differences within a climax vegetation (Dyksterhuis 1949; Shiflet 1973). In some mapping instances, a range site may be delineated on the basis of a nonecological interpretation, such as extremely rocky or extremely steep, which may have important management implications (Shiftlet 1973; USDA 1976). In recent years, the term "ecological site" has been used in place of range site (Anderson 1983).

The third unit of classification is the community type (Mueller-Dombois and Ellenberg 1974; Shimwell 1976). It is an ecological classification based on current vegetation and is not specific as to its successional status (Whittaker 1975; Shimwell 1976; Youngblood and Mueggler 1981). Thus, community type classification is able to handle disturbed communities, of which we have so many.

The three classification schemes have been used in classifying and delineating (mapping) our sagebrush ranges singularly. At times, overlays of two of the three classification schemes have been used, but rarely has the information contained in the overlays of all three systems been used simultaneously.

IMPORTANCE OF PLANT SPECIES IDENTIFICATION

Identification of dominant and prominent species has been basic in the development of the three classification schemes. Without the recognition of subspecies of *Artemisia tridentata*, development of accurate land classification schemes would be difficult, if not impossible. This taxon is the dominant shrub species occupying vastly different kinds of effective environments. It is the dominant species in areas that receive 8 to 20 inches (200 to 500 mm) of annual precipitation, spans an elevational gradient from 600 ft to more than 10,000 ft (180 to 3 300 m) and occurs on all major nonforest soils in the Intermountain Region.

The recognition of ecologically meaningful subspecies in *Artemisia tridentata* by Beetle (1959, 1960) and Beetle and Young (1965) permitted the development of the habitat type classification of the sagebrush region (Hironaka and others 1983). The subspecies *wyomingensis*, *vaseyana*, and *tridentata* are excellent diagnostic taxa because of their consistent relation to climate and soil conditions.

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RANGE SITE CLASSIFICATION PRIOR TO 1965

One might wonder how the range site classification, as perceived by Dyksterhuis (1949, 1958), was workable in the sagebrush region prior to the recognition of subspecies in Artemisia tridentata. Prior to 1965, it was to a large extent by chance that range sites coincided with the distribution of the yet-to-be-recognized subspecies. A separation of range sites was arbitrarily established at the 12-inch (300 mm) isohyet (average annual precipitation) which coincided fairly near the division in the distribution of subspecies wyomingensis and subspecies vaseyana. The highly productive range sites on deep soils agreed with the occurrence of subspecies tridentata. The division of range regions into physiographic provinces (USDA 1976) helped further in stratifying sites and effective environments. Range site, as mentioned earlier, is based on the climax vegetation as is habitat type. Within a climax vegetation, there is variation in productivity due to soil differences. Range site stratifies the different productivity levels within a climax vegetation, with each level constituting a different range site. In reality, the range site is a subdivision within a habitat type, based on productivity or uniformity in species composition (Hironaka and others 1983).

CLASSIFICATION CONTROVERSY

Recently, one hears that habitat type and range site are the same, or there is no need for both classification schemes in range management (Dyksterhuis 1983). One also hears that habitat type classification should be restricted to forest vegetation and should not be used in classification of rangelands, or habitat type is based on climax vegetation whereas range site classification is based on soils. All of these statements are incorrect; habitat type and range site are not the same (Hironaka and others 1983). Habitat type classification can be used for forest and rangeland (Daubenmire 1952; Daubenmire 1973; Mueggler and Stewart 1980; Hironaka and others 1983). Both classifications are based on climax vegetation, and both are associated with unique sets of soils, with particular reference to the soil series and soil series phase level of soil classification (Hironaka and others 1983). So what is the controversy? From a philosophic viewpoint, Dyksterhuis (1958, 1983) states that the range site concept is based on the premise that climax vegetation is a continuum, whereas habitat type as defined by Daubenmire (1968, 1978) views climax vegetation as being composed of discrete communities. Other than the difference in philosophic viewpoint on whether climax communities are discrete or form continua, the two approaches to classification are basically the same. Whether one accepts the continuum or the discrete community concept (Curtis 1958; Whittaker 1960; Daubenmire 1978), the classification units remain unchanged, so I cannot see how one classification scheme or the other is invalidated.

IMPORTANT DIFFERENCES

Although the basic floristic composition of habitat type and range site of the climax vegetation is similar, the species composition and site productivity within the bounds of a range site is more homogeneous than that of a habitat type. The range site is a homogeneous subdivision of a habitat type based on uniformity of productivity or species composition. The uniformity of effective environment is evidenced by greater similarity of soils with than between range sites (Heerwagen and Aandahl 1961). The range site is comparable to habitat type phase (Pfister and others 1977; Hironaka and others 1983).

Community type classification is generally used without reference to climax or potential natural vegetation and often gives the impression that it is wholly different and independent of the other two classification schemes. In reality, community types are related to range sites and habitat types, but not uniquely.

A UNIFYING SCHEME

Proper interpretation and use of these classification schemes can provide the wherewithal to do something monumental for land management. Unifying and incorporating the three schemes into a simple hierarchical scheme can be the basis for a sound information storage-retrieval system for land management. Prior to the introduction of habitat type classification, there was no basis by which range sites could be ecologically aggregated. As initially conceived, each range site was an independent unit with no relation to other range sites. The habitat type permits the grouping of range sites with the same basic climax vegetation, but differing productivities because of soil differences. The soils associated with specific range sites are in turn associated with specific habitat types. Thus, each range site is associated with a unique set of soils. The same is the case with each habitat type.

INFORMATION STORAGE-RETRIEVAL SYSTEM

If the community types that occur in each range site and habitat type are identified and their responses to management are documented, the information could be stored and provide a library of information for later retrieval. Prior to habitat type classification, there was no ecological basis by which range sites could be aggregrated. True, range sites could be grouped as to precipitation zone, land form, topographic position, and other site features, but with no reference to vegetation, potential or otherwise. As originally developed, range site classification was not a part of a hierarchical system, but one of independent units. Habitat type classification permits range sites with the same basic climax vegetation, but different productivity levels, to be grouped together. With this information,

productivity levels within habitat type can be identified. In addition, if the associated community types are identified and characterized, there would be available much information concerning any landscape that had been classified. The boundaries of habitat type and range site remain permanent for all practical purposes. The only changing unit is the community type as the vegetation undergoes changes because of secondary succession, retrogression, or drastic vegetational alteration without excessive change in site potential. As information is documented for a particular community type, it is filed and cataloged by habitat type and range site for later retrieval.

Each land management district can have available an inventory of habitat types, their associated range sites and community types as well as soils and other site and management implication information. This would enable recall of any community type in relation to specific range sites and habitat types and have available much pertinent land management information based on the first-hand experiences of many land managers. For the first time, a means would be available by which this type of information could be filed and retrieved so that each succeeding land manager could build on what was learned by his predecessors on comparable landscapes rather than rely on his own experiences. As new experiences and information are gained, they are added to the library of information.

This becomes the ultimate use of the three classifications. Each by itself has limited value, but when the three schemes are viewed as members of a larger system, it enables the development of a comprehensive information storage-retrieval system on an ecological base for land management. All three classification schemes are needed to classify our rangelands. They are not duplications; each provides different kinds of information about the land and the vegetation it supports or supported. No one scheme is better than the other. All are needed for the wise management of our rangelands.

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In: McArthur, E. Durant; Welch, Bruce L., compilers. Proceedings--symposium on the biology of Artemisia and Chrysothamnus; 1984 July 9-13; Provo, UT. General Technical Report INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986. 398 p.

Section 2. Genetics, Systematics, and Synecology

TAXONOMIC AND GEOGRAPHIC LIMITS OF ARTEMISIA SUBGENUS TRIDENTATAE (BEETLE) MCARTHUR (ASTERACEAE: ANTHEMIDEAE)

Leila M. Shultz

ABSTRACT: Illustrations, distribution maps, and ecological notes are presented as an aid to identification of sagebrush. An historical background outlines some of the nomenclatural development of the complex leading to the current classification of taxa presented here.

HISTORICAL BACKGROUND

Rydberg (1916) considered members of Tridentatae as three sections within the subgenus Seriphidium. These sections were Tridentatae (11 species), Rigidae (1 species), and Pygmaeae (1 species).

In the most conservative treatment of the group, Hall and Clements (1923) recognized only five species, with seven subspecies, in the section Seriphidium. Following the division of the genus into four sections by Besser (1829), Hall and Clements considered Artemisia bigelovii as a member of section Abrotanum that was transitional to section Seriphidium. They also included Artemisia palmeri in section Seriphidium.

In a cytogenetic study of the species, Ward (1953) recognized eight species and 11 subspecies in the western North American Seriphidia. Ward included A. palmeri A. Gray as a member of section Seriphidium, and A. bigelovii A. Gray as a member of the Abrotanae. Beetle (1960) preferred to treat the complex as the section Tridentatae and questioned the relationship to European members of the section Seriphidium.

McArthur (McArthur and others 1981) elevated section Tridentatae to subgeneric status, adding a fifth subgenus to Artemisia. I have adopted this subgeneric classification, differing from McArthur only in the transfer of A. bigelovii and A. palmeri to the subgenus Artemisia which is the old section Abrotanae (Shultz 1983). I consider the inclusion of A. pygmaea the only enigmatic consideration in circumscribing the Tridentatae as a natural, monophyletic group.

DISCUSSION

The specific and intraspecific taxonomy of sagebrush remains controversial. Considering the complexity of the group, this situation is unlikely to change. The complex is in a dynamic state of expansive evolution and hybridization among species and subspecies is common. The precise definition of species, therefore, becomes obscured and rests in part on individual evolutionary philosophy. Controversy exists primarily at the intraspecific level in the division of subspecies and varieties.

Morphological entities display a remarkable fidelity to certain habitats and hybridization among populations occurs primarily at the interface of these habitats. Thus, in an evolutionary sense, we can see morphological specializations and adaptations along environmental gradients. For the most part, there is consensus among field workers in the Intermountain region concerning identification of the basic groups and the ecological integrity of different types of sagebrush. However, one may become easily confused in making identifications because of the great morphological similarity of the groups. The illustrations, distribution maps, and ecological notes in this paper are offered as a simplified means to identification of the species and subspecies of sagebrush.

Dots on the maps represent several thousand collections that I have examined and verified at the herbaria of the institutions listed below. Populations that have not been documented in collections are not included, and certainly, these maps may stimulate the report of important records. I welcome all correspondence. A complete file of specimen citations is maintained at the Intermountain Herbarium. I am grateful to the curators at the following institutions who have graciously permitted access to all files:

Brigham Young University
California Academy of Sciences
University of California at Berkeley
Colorado State University
University of Colorado
University of Idaho*
Gray Herbarium at Harvard*
Missouri Botanical Garden
New York Botanical Garden*
Oregon State University*
Rancho Santa Ana Botanical Garden
Smithsonian Institution (U.S. Natl. Herbarium)*

Paper presented as an invited postscript to the symposium: Biology of Artemisia and Chrysothamnus, Provo, UT, July 9-13, 1984.

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University of Utah
Utah State University (Intermountain Herbarium)
Washington State University*
University of Washington*
University of Wyoming (Rocky Mountain Herbarium)*

*Asterisks indicate collections in which sagebrush collections were only partially examined and recorded.

SPECIES AND SUBSPECIES OF ARTEMISIA SUBGENUS TRIDENTATAE, WITH ECOLOGICAL NOTES

1. (a) Artemisia arbuscula Nutt. ssp. arbuscula, Trans. Am. Phil. Soc. 2(7): 398. 1884. Occurs on rocky, shallow soils, such as rock ridges and other sites swept free of snow by winds, in the mountains. The leaves on the flowering stem are lobed, as are other subspecies of Artemisia arbuscula.

   (b) A. arbuscula Nutt. ssp. longiloba (Osterh.) L. Shultz, ined. Occurs on fine-textured clay basins in the valley and mountains. Morphologically, this subspecies is very similar to typical arbuscula although it is reproductively isolated by blooming time. This is the only taxon that blooms in late spring and early summer rather than late summer to fall.

   (c) A. arbuscula Nutt. ssp. thermopola Beetle, Rhodora 61:83. 1959. Habitat as for subspecies arbuscula. Varies morphologically in having more finely divided leaves, and being restricted to areas adjacent to those occupied by A. tripartita, with which A. arbuscula may have hybridized to form the subspecies thermopola.

2. (a) Artemisia cana Pursh ssp. cana, Fl. Amer.: 521. 1814. Occupies sandy soils of prairies and along streams, in valleys east of the Continental Divide.

   (b) A. cana Pursh ssp. bolanderi (A. Gray) Ward, Contr. Dud. Herb. 4(8):192. 1953. Found primarily in the Sierra Nevada Mountains of California, barely entering Oregon and Nevada. Similar to A. cana ssp. viscidula, from which it varies in its dense tomentum on the stem. Occurs along streams and in snow catchment basins, on granitic soils.

   (c) A. cana Pursh. ssp. viscidula (Osterh.) Beetle, Rhodora 61:84. 1959. Habitat of moist meadows and snow-catchment basins in mountains east of the Sierra Nevadas, usually on limestone-derived soils. I include A. argillosa Beetle with this subspecies.

3. Artemisia nova A. Nels., Bull. Torr. Club 27:274. 1900. Found in desert valleys and mountain slopes (south and west exposures), on shallow lithosols overlying bedrock.

4. Artemisia pygmaea A. Gray, Proc. Am. Acad. 21:413. 1886. Restricted to shale-barrens at low elevations within the Great Basin of Nevada and Utah and Uinta Basin of Utah and Colorado (first collection in Colorado reported by Shultz [1983]).

5. Artemisia rigida (Nutt.) A. Gray, Proc. Am. Acad. 19:49. 1883. Grows on basalt scablands of the Columbia Basin of eastern Washington, Oregon, and extreme western Idaho.

6. Artemisia rothrockii A. Gray, Bot. Calif. 1:618. 1876. Endemic to California in the southern Sierra Nevada and San Bernardino Mountains where it is found in high elevation silt basins and on rocky slopes. I consider collections from the Intermountain region previously referred to as A. rothrockii as A. X spiciformis.

7. Artemisia X spiciformis Osterh, Bull. Torr. Club 27:507. 1900. The "X" designates this taxon as a hybrid. Because the populations are stable and apparently reproducing (see McArthur and Goodrich, this proceedings), it is worthy of formal taxonomic status. A. spiciformis is often considered a subalpine form of Vasey sagebrush, although I consider it to be a hybrid of A. cana ssp. viscidula and A. tridentata ssp. vaseyana at most sites. In Colorado, at the type locality of A. spiciformis, A. arbuscula may be a putative parent. Because of the need for experimental work with this taxon and the uncertain nature of hybridity, I leave this taxon with the name previously published by Osterhout rather than use the subspecies designation proposed by Goodrich and others (1985). The illustration shows leaf and floral features which are obviously intermediate between subspecies A. cana ssp. viscidula and A. tridentata ssp. vaseyana.

8. (a) Artemisia tridentata Nutt. ssp. tridentata, Trans. Am. Phil. Soc. 2(7):398. 1841. This is the common big sagebrush of valleys and foothills. It occurs in deep, well-drained sandy or gravelly soils.

   (b) A. tridentata Nutt. ssp. parishii (A. Gray) Hall & Clements, Carn. Inst. Wash. Publ. 326:137. 1923. This taxon is distinguished by its hairy achenes and usually drooping flower branches. It is restricted to the coastal ranges and cismontane region of California.

(c) A. tridentata Nutt. ssp. vaseyana (Rydb.) Beetle, Rhodora 61:83. 1959. Vasey sagebrush is the most common and abundant sagebrush in the West. It is often the dominant shrub on mountain slopes and occurs throughout the Rocky Mountains and Intermountain West, from low benches into the alpine zone, usually on rocky soils. Its wide ecological diversity is reflected in a sometimes bewildering array of morphological forms.

(d) A. tridentata Nutt. ssp. wyomingensis Beetle & Young, Rhodora 67:405. 1965. Wyoming sagebrush may be the most difficult to recognize of the various subspecies. The short, narrow flower clusters and "twiggy" appearance are characteristic of tetraploid populations. Polyploidy apparently contributes to the ability of this plant to colonize drier sites than those occupied by A. tridentata ssp. tridentata.

9. (a) Artemisia tripartita Rydb. ssp. tripartita, Mem. N.Y. Bot. Gard. 1:432. 1900. Occurs on deep, well-developed loam soils, in valleys, primarily on the fertile volcanic soils of Idaho. Much of this area has been plowed for farmland, which accounts for what may seem to be a spotty distribution.

(b) A. tripartita Rydb. ssp. rupicola Beetle, Rhodora 61:60. 1959. Differs from typical tripartita in having a dwarfed growth form and preference for drier habitat. Occurs on shallow, rocky soils east of the Continental Divide, usually on barren knolls surrounded by well-developed grasslands.

ACKNOWLEDGMENTS

I am grateful to Steven Cannon for carefully executed illustrations and to Mary Bybee and Bryan Hammond for their help in preparing distribution maps. I also thank Drs. Durant McArthur and Al Winward, Prof. Arthur Holmgren and Sherel Goodrich who have provided many stimulating conversations on sagebrush taxonomy.

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Map 1 (a). Distribution of *Artemisia arbuscula* ssp. *arbuscula*.

Artemisia arbuscula ssp. *arbuscula*

Map 1 (b). Distribution of *Artemisia arbuscula* ssp. *longiloba*.

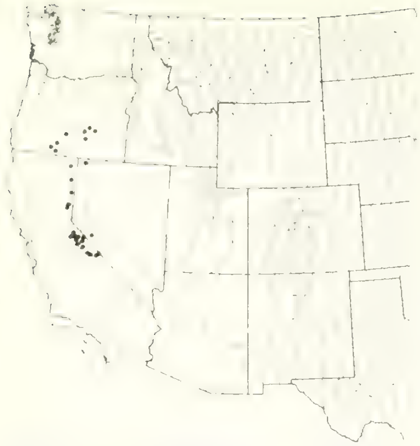
Artemisia arbuscula ssp. *longiloba*

Map 1 (c). Distribution of *Artemisia arbuscula* ssp. *thermopola.*

Artemisia arbuscula ssp. *thermopola*

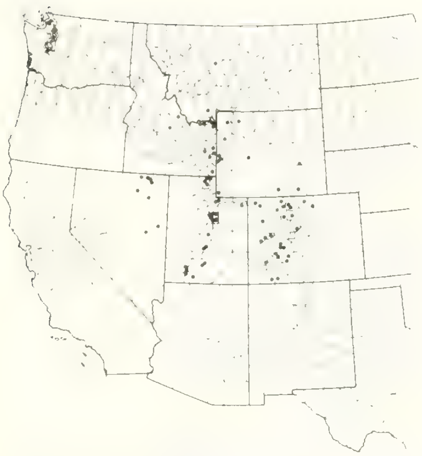
Map 2 (a). Distribution of *Artemisia cana* ssp. *cana.*

Artemisia cana ssp. *cana*



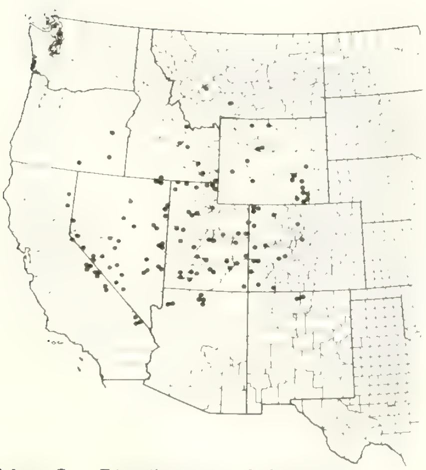
Map 2 (b). Distribution of *Artemisia cana* ssp. *bolanderi.*

Artemisia cana ssp. *bolanderi*



Map 2 (c). Distribution of *Artemisia cana* ssp. *viscidula.*

Artemisia cana ssp. *viscidula*



Map 3. Distribution of *Artemisia nova.*

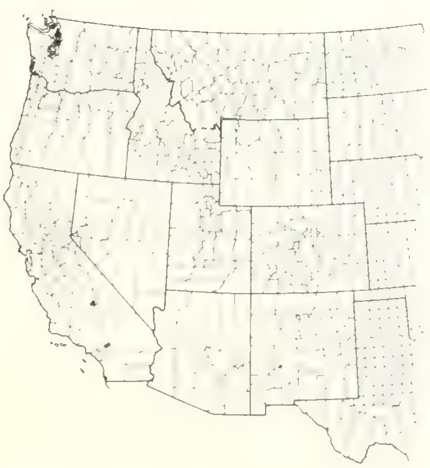
Artemisia nova

Map 4. Distribution of *Artemisia pygmaea.*

Artemisia pygmaea

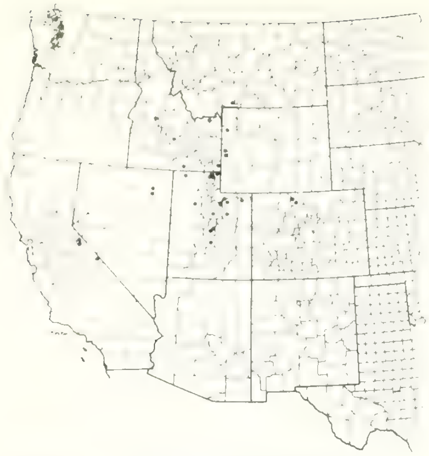
Map 5. Distribution of *Artemisia rigida.*

Artemisia rigida



Map 6. Distribution of *Artemisia rothrockii.*

Artemisia rothrockii



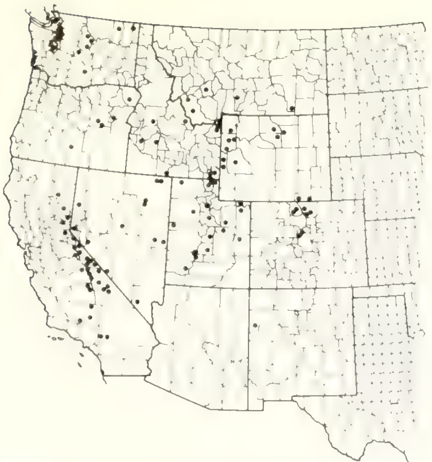
Map 7. Distribution of *Artemisia* X *spiciformis.*

Artemisia x *spiciformis*

Map 8 (a). Distribution of *Artemisia tridentata* ssp. *tridentata.*

Artemisia tridentata ssp. *tridentata*

Map 8 (b). Distribution of *Artemisia tridentata* ssp. *parishii.*

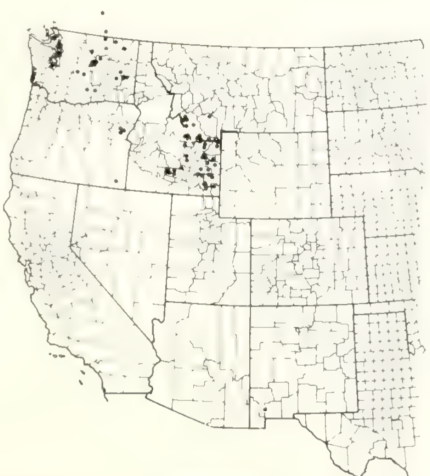


Map 8 (c). Distribution of *Artemisia tridentata* ssp. *vaseyana.*

Artemisia tridentata ssp. *vaseyana*

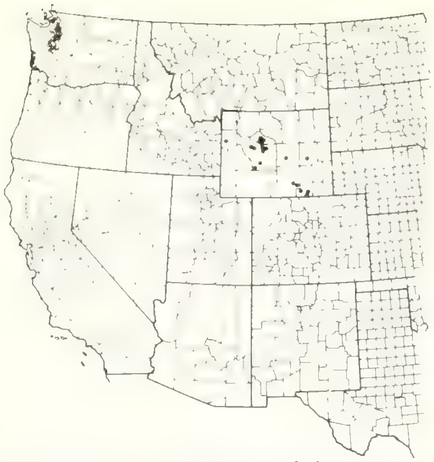
Map 8 (d). Distribution of *Artemisia tridentata* ssp. *wyomingensis.*

Artemisia tridentata ssp. *wyomingensis*



Map 9 (a). Distribution of *Artemisia tripartita* ssp. *tripartita.*

Artemisia tripartita ssp. *tripartita*



Map 9 (b). Distribution of *Artemisia tripartita* ssp. *rupicola.*

Artemisia tripartita ssp. *rupicola*

In: McArthur, E. Durant; Welch, Bruce L., compilers. Proceedings--symposium on the biology of Artemisia and Chrysothamnus; 1984 July 9-13; Provo, UT. General Technical Report INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986. 398 p.

AN OVERVIEW OF THE GENUS CHRYSOTHAMNUS (ASTERACEAE)

Loran C. Anderson

ABSTRACT: The genus Chrysothamnus contains five sections, 16 species, and 41 subspecies. General comments, keys to the species and subspecies, and an atlas of distributional maps are given.

INTRODUCTION

Chrysothamnus (commonly known as rabbitbrush) is a widespread genus over much of western North America. Some species are sub-dominants in sagebrush desert and desert grassland; others are truly montane. This overview is provided now in anticipation of my upcoming monograph, which will include much more detail. The early nomenclatural history of the genus was summarized by Hall and Clements (1923). They recognized four sections, 12 species, and 40 subspecies.

Subsequent work has resulted in additional resolution of the taxonomy. For example, C. pyramidatus was transferred to Haplopappus (Blake 1926) and finally to Baccharis (Rzedowski 1972). Chrysothamnus gramineus was reclassified as a Petradoria (Anderson 1963). New species include C. eremobius, C. molestus, and C. spathulatus (Anderson 1964, 1983). Chrysothamnus linifolius and C. humilis are recognized as distinct species again. One fossil species, C. pulchelloides, has been recorded for the genus (Anderson 1980c). In addition, several new subspecies have been described (Anderson 1978, 1980a, 1980b, 1981, 1984), and sectional composition within the genus has been modified.

The transfer of C. gramineus to Petradoria (as P. discoidea) was made with the knowledge available at that time. With the recent discovery of C. eremobius (Anderson 1983), it is apparent that C. gramineus should be retained in Chrysothamnus. A new section of the genus is formally described to accommodate the species C. eremobius and C. gramineus (type species of the section).

Chrysothamnus Gramini L. C. Anderson, sect. nov.

Caules recti annui e caudice lignoso crescentes; folia plana, rigida, chartaceae, manifeste venosa, plusminusve persistentia.

Sectional composition in Chrysothamnus is now perceived as follows:

Section Chrysothamnus
- C. albidus (Jones ex Gray) Greene
- C. greenei (Gray) Greene
- C. humilis Greene
- C. linifolius Greene
- C. spathulatus L. C. Anderson
- C. viscidiflorus (Hook.) Nutt.

Section Gramini
- C. eremobius L. C. Anderson
- C. gramineus Hall

Section Nauseosi
- C. parryi (Gray) Greene
- C. nauseosus (Pallas) Britt.

Section Pulchelli
- C. depressus Nutt.
- C. molestus (Blake) L. C. Anderson
- C. pulchellus (Gray) Greene
- C. vaseyi (Gray) Greene

Section Punctati
- C. paniculatus (Gray) Hall
- C. teretifolius (Dur. & Hilg.) Hall & Clem.

Characteristics of the sections are given in the key to the species. Presumed phylogenetic relationships of taxa within and among sections are given in Anderson and Fisher (1970) and Anderson (1983). Figure numbers precede taxon name in right-hand column.

Paper presented at the Symposium: Biology of Artemisia and Chrysothamnus, Provo, UT, July 9-13, 1984.

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KEY TO THE SPECIES

1. Stems tomentose, hairs often densely compacted (Section Nauseosi)

   2. Phyllaries attenuate, weakly keeled, rather membranous; inflorescences mostly racemose; heads 5-20 flowered . . . . C. parryi (12 ssp.)

   2. Phyllaries obtuse to acute, if attenuate then strongly keeled, chartaceous; inflorescences mostly cymose; heads usually 5 flowered . . . . C. nauseosus (22 ssp.)

1. Stems glabrous, puberulent, or resinous-punctate, never tomentose

3. Stems and leaves resinous-punctate; corollas yellow (Section Punctati)

4. Involucres 6-8 mm long, turbinate; phyllaries weakly aligned vertically . . 19. C. paniculatus

4. Involucres 7.6-9.5 mm long, cylindric; phyllaries strongly aligned vertically with swollen tips . . . . 26. C. teretifolius

3. Stems not resinous-punctate, if leaves resinous-punctate then corollas white

5. Upright stems annual; leaves flat, rigid, strongly veined, more or less persistent (Section Gramini)

6. Involucres 11-17.5 mm long; phyllaries not keeled; achenes glabrous . . 3. C. gramineus

6. Involucres 6.5-9 mm long; phyllaries keeled; achenes pubescent . . . . . 3. C. eremobius

5. Upright stems perennial; leaves often twisted, not rigid, strongly veined if persistent

7. Achenes glabrous with few glands just below pappus or few hairs along ridges (Section Pulchelli)

8. Corollas less than 9 mm long, surpassing the pappus

9. Involucres 5-7 mm long; phyllaries weakly aligned and keeled . . . 27. C. vaseyi

9. Involucres 10-13 mm long; phyllaries strongly aligned and keeled

10. Leaves less than 2 mm wide, densely glandular-hispid . . . . . 6. C. molestus

10. Leaves more than 2 mm wide, hispid or glabrous, rarely sparsely glandular . . . . 2. C. depressus

8. Corollas mostly over 9 mm long but surpassed by abundant pappus . . . C. pulchellus (2 ssp.)

7. Achenes densely pubescent, rarely sparsely so in C. humilis and C. spathulatus but then achenes not ridged (Section Chrysothamnus)

11. Corollas white; leaves resinous punctate . . . . 1. C. albidus

11. Corollas yellow; leaves more or less resinous, never punctate

12. Heads often overtopped by leaves; flowers 2-3(4); style branches included or barely surpassing corolla lobes, appendages long . . 5. C. humulis

12. Heads not overtopped by leaves; flowers 3 or more; styles long exserted beyond spreading corolla lobes

13. Style appendages long (40-70% of style branch); leaves lanceolate or spatulate, never twisted; shrubs over 7 dm tall

14. Involucres less than 6 mm long, turbinate; leaves lanceolate; plants soboliferous; achenes densely pubescent . . . . . 6. C. linifolius

14. Involucres over 6 mm long, cylindric; leaves spatulate; plants never soboliferous; achenes sparsely pubescent . 26. C. spathulatus

13. Style appendages short (30-45% of style branch); leaves linear to oblong-lanceolate, frequently twisted or involute

15. Phyllaries acuminate-cuspidate; leaves 1-2 mm wide . . . 4. C. greenei

15. Phyllaries obtuse or acute; leaves 1-10 mm wide . . . . C. viscidiflorus (5 ssp.)

The species are fairly well defined, but a few of them have considerable intraspecific variability, which has resulted in differing taxonomic treatments as seen in table 1.

Table 1.--The complex taxa of Chrysothamnus

Species	Total names as species	Subspecies number (Hall and Clements 1923)	Subspecies number (Anderson this paper)
C. nauseosus	62	20	22
C. parryi	15	10	12
C. viscidiflorus	25	9	5

KEY TO THE SUBSPECIES

Chrysothamnus nauseosus

1. Involucres pubescent to tomentose, rarely nearly glabrous; stems mostly whitish with tomentum; leaves mostly dark green or grayish-white ("gray group")

2. Achenes glabrous, at least on lower half

3. Achenes with tuft of hairs just below pappus; phyllaries sparsely villous as well as tomentose . . . . 18. ssp. *washoensis*

3. Achenes totally glabrous; phyllaries tomentose to nearly glabrous

4. Leaves linear; corollas over 9 mm long

5. Pappus about equal to corolla in length; style appendages longer than stigmatic portion . . . . 9. ssp. *bigelovii*

5. Pappus much shorter than corolla; style appendages shorter than stigmatic portion . . . . 17. ssp. *texensis*

4. Leaves narrowly oblanceolate; corollas less than 9 mm long . . . . . 17. ssp. *psilocarpus*

2. Achenes densely pubescent

6. Leaves 3-10 mm wide; phyllaries mostly obtuse . . . . 17. ssp. *salicifolius*

6. Leaves 1-3 mm wide; phyllaries various, usually acute

7. Outer phyllaries densely tomentose, inner ones glabrous

8. Plants mostly 1-2 dm tall; corolla lobes 1-2.5 mm long

9. Involucres 8-9 mm long; corolla lobes 1.6-2.5 mm long . . . . 15. ssp. *nanus*

9. Involucres 11-13 mm long; corolla lobes 1-1.5 mm long . . . . 18. ssp. *uintahensis*

8. Plants over 3 dm tall; corolla lobes 0.5-1 mm long . . . . 14. ssp. *latisquameus*

7. All phyllaries tomentose, sometimes sparsely so

10. Involucres 7-10(11) mm tall

11. Corolla lobes 1-2 mm long; style appendages longer than stigmatic portions

12. Corollas 6-8.5 mm long; involucres 7-9.5 mm long; shrubs mostly 2-6 dm tall . . . . 16. ssp. *nauseosus*

12. Corollas (8)9-11 mm long; involucres mostly 9-11 mm long; shrubs 4-15 dm tall (lower in some alpine forms) . . . . 7. ssp. *albicaulis*

11. Corolla lobes 0.5-1 mm long; style appendages shorter than stigmatic portions . . . . 12. ssp. <u>hololeucus</u>

10. Involucres 11-13 mm long

13. Corolla lobes 1.7-2.3 mm long, glabrous . . . . 8. ssp. <u>bernardinus</u>

13. Corolla lobes 0.5-1 mm long, villous . . . . 18. ssp. <u>turbinatus</u>

1. Involucres glabrous, outer phyllaries sometimes ciliate or scurfy; stems greenish, tomentum more compacted; leaves usually greenish-yellow or absent ("green group")

14. Achenes glabrous

15. Outer phyllaries scurfy tomentulose, obtuse; inner ones glabrous, weakly keeled; stems yellowish-green . . . . 16. ssp. <u>nitidus</u>

15. Outer phyllaries glabrous, obtuse to acute, keeled; stems brownish to grayish-green

16. Involucres 7.5-10.5 mm long; stems often leafless . . . . 14. ssp. <u>leiospermus</u>

16. Involucres 12-16 mm long; stems very leafy . . . . 13. ssp. <u>iridis</u>

14. Achenes pubescent

17. Involucres over 15 mm long; phyllaries strongly keeled and cuspidate 8. ssp. <u>arenarius</u>

17. Involucres less than 15 mm long; phyllaries not cuspidate

18. Leaves 1-3 mm wide, 1-5-nerved

19. Involucres 11-13 mm long; corolla lobes 1.7-2.3 mm long . . . 8. ssp. <u>bernardinu</u>

19. Involucres 6.7-9.5 mm long; corolla lobes 0.6-1.5 mm long . . 11. ssp. <u>graveolens</u>

18. Leaves 1 mm wide or less, 1-nerved

20. Phyllaries abruptly pointed, recurved . . . . 9. ssp. <u>ceruminosu</u>

20. Phyllaries acute, erect

21. Involucres 7-8 mm long; stems usually leafy; corolla lobes glabrous (achenes sometimes glabrous in Idaho) . . . . . 10. ssp. <u>consimilis</u>

21. Involucres 9-10 mm tall, phyllaries strongly ranked; stems often leafless

22. Corolla lobes glabrous . . . . 15. ssp. <u>mohavensis</u>

22. Corolla lobes villous (sometimes sparsely so) . . . . 13. ssp. <u>junceus</u>

<u>Chrysothamnus parryi</u>

1. Flowers mostly 8-20 per head or leaves over 5 mm wide (never with stalked glands)

2. Shrubs over 3 dm tall; leaves mostly over 3 cm long

3. Flowers 8-20 per head; leaves 2-3 mm wide . . . . 24. ssp. <u>parryi</u>

3. Flowers 5-7 per head; leaves 5-14 mm wide . . . . 22. ssp. <u>latior</u>

2. Shrubs 1-2 dm tall; leaves mostly less than 3 cm long

4. Leaves 2-3.5 cm long, overtopping the inflorescence; corollas 9-10 mm long . . . . 23. ssp. <u>montanus</u>

4. Leaves 1-1.5 mm long, not overtopping inflorescence; corollas 10-12 mm long . . . . 22. ssp. <u>imulus</u>

1. Flowers mostly 5-7 per head; leaves 1-3 mm wide (flowers up to 10 per head and leaves to 4 mm wide in ssp. asper, then leaves with stalked glands)

5. Leaves oblanceolate, with short stalked glands; corollas up to 9 mm long . 20. ssp. asper

5. Leaves linear to oblanceolate, without stalked glands

6. Inflorescences reduced to 1-2 heads, each with 8-11(13) phyllaries; corollas 8-9 mm long . . . . 22. ssp. monocephalus

6. Inflorescences with many heads; corollas mostly over 9 mm long

7. Inflorescences lax and elongated; involucres 12.5-15 mm long with 9-13 straight, narrow phyllaries . . . . 24. ssp. vulcanicus

7. Inflorescences more compact; involucres shorter or with more phyllaries, often broader, spreading or recurved

8. Upper leaves overtopping inflorescence; corollas pale yellow, mostly 8-10 mm long

9. Inflorescences somewhat elongate, sparsely leafy; involucres 10-12 mm long; corolla lobes 1-1.5 mm long . . . . 24. ssp. salmonensis

9. Inflorescences compact, very leafy; involucres 11.5-16 mm long; corolla lobes 1.5-1.7 mm long . . . . 21. ssp. howardii

8. Upper leaves shorter than inflorescence; corollas often over 10 mm long

10. Corollas pale yellow, tubes abruptly dilated; corolla lobes 0.7-1 mm long, lanceolate . . . . 20. ssp. affinis

10. Corollas clear yellow, tubes gradually flaring; corolla lobes 1.5-2 mm long, relatively broader

11. Phyllaries mostly straight tipped; involucres 11-15 mm long . . . . 21. ssp. attenuatus

11. Phyllaries with recurved tips; involucres 14-19 mm long . 23. ssp. nevadensis

Chrysothamnus pulchellus

1. Shrubs 8-12 dm tall; leaves glabrous or puberulent, margins entire; corollas 11-13 mm long . . . . 25. ssp. pulchellus

1. Shrubs 0.5-5(7) dm tall; leaves with scabrous-ciliolate margins, otherwise glabrous; corollas 7-12 mm long . . . . 25. ssp. baileyi

Chrysothamnus viscidiflorus

1. Leaves planate, glabrous; corollas 3.5-4(4.5) mm long . . . . 30. ssp. planifolius

1. Leaves more or less twisted or pubescent or corollas longer

2. Upper stems, frequently leaves, hairy

3. Stems and leaves finely puberulent; leaves 1-2(4) mm wide . . . . 30. ssp. puberulus

3. Stems hispid near inflorescence; leaves over 2 mm wide, hirsute or glabrous . . . . 29. ssp. lanceolatus

2. Stems glabrous; leaves often with ciliate margins, otherwise glabrous

4. Leaves ± 1 mm wide; flowers 3-4(5) per head; involucres somewhat turbinate . . . . 28. ssp. axillaris

4. Leaves 1-10 mm wide; if 1 mm then flowers 4 or more per head and involucres narrowly cylindric . . . . 31. ssp. viscidiflorus

NAMES EXCLUDED FROM THE KEYS

Chrysothamnus nauseosus ssp. glareosus (Jones) Hall & Clem.: taxon described as having glabrous achenes and flowers a half inch long, from Marysvale, UT. No specimens have been located in the herbaria or in the field.

Chrysothamnus nauseosus ssp. viscosus Keck: taxon described as differing somewhat from ssp. hololeucus. Type collection is an intergeneric hybrid between ssp. hololeucus and Haplopappus cuneatus.

Chrysothamnus parryi ssp. bolanderi (Gray) Hall & Clem.: known only from type locality. It is an intergeneric hybrid between C. nauseosus ssp. albicaulis and Haplopappus marconema.

NOMENCLATURAL INFORMATION AND TRIVIA

Figure

1. C. albidus (Jones ex Gray) Greene. The only white-flowered and most resinous species in the genus. Its geographical range is extensive, but it is not particularly abundant anywhere.

2. C. depressus Nutt. Somewhat variable species with stouter forms in Nevada and California, but there are no correlated patterns of variability worthy of taxonomic recognition.

3. C. eremobius L. C. Anderson. This very distinctive species was only recently discovered and described. Vegetatively it looks somewhat like Petradoria pumila.

3. C. gramineus Hall. This species was transferred to Petradoria by me several years ago based on then current data. Morphology of C. eremobius warrants returning this species to Chrysothamnus.

4. C. greenei (Gray) Greene. The species is very closely related to C. viscidiflorus. Narrow-leaved forms have been called ssp. filifolius, but leaf width varies under garden culture. I choose not to recognize the subspecies. It could be recognized at the varietal level.

5. C. humilis Greene. The earliest blooming species in the genus, it is sometimes confused with C. viscidiflorus ssp. puberulus, from which it can be distinguished by its coarser vesture in addition to the key characters and more cryptic anatomical features.

6. C. linifolius Greene. The only species in the genus that is soboliferous, it also has some unique anatomy--clearly distinct from C. viscidiflorus.

6. C. molestus (Blake) L. C. Anderson. This rare species is distinctive in the genus with its glandular-hispid foliage.

C. nauseosus (Pallas) Britt. The most complex and wide-ranging species in the genus. I have merged some of the subspecies of Hall and Clements but have also described new ones. Names of varieties within the more complex subspecies will be given in the upcoming monograph for those who wish further details of interrelationships. Twenty-two subspecies are currently recognized; they are sometimes subdivided as the "gray group" and the "green group" based on density of tomentum of stems and leaves. That categorization is not very good because individual plants of ssp. bernardinus fit one group or the other, and considerable variation in tomentum density can occur within a given population in several subspecies.

7. ssp. albicaulis (Nutt.) Hall & Clem. Includes the names californicus, macrophyllus, and speciosus. Perhaps the most variable ssp. in C. nauseosus, it intergrades somewhat with ssp. consimilis, nauseosus, and especially hololeucus where their ranges overlap.

8. ssp. arenarius L. C. Anderson. Very distinctive with heads up to 20 mm long and phyllaries strongly keeled. Recently found in Mesa Co., CO (new to that state), but not shown on map.

8. ssp. bernardinus (Hall) Hall & Clem. Very close to ssp. albicaulis.

9. ssp. bigelovii (Gray) Hall & Clem. Very distinctive, but rarely mistaken for C. parryi spp. howardii.

9. ssp. cerminosus (Dur. & Hilg.) Hall & Clem. Looks like a ssp. consimilis or mohavensis but with prominently recurved phyllary tips.

10. ssp. consimilis (Greene) Hall & Clem. Includes names artus, oreophilus, petrophilus (a form with glabrous achenes), pinifolius, and viridulus. Several of these are worthy of varietal status within the subspecies.

11. ssp. graveolens (Nutt.) Piper. Includes names confinis, falcatus, glabrata, and nivecaulis. Intergrades with ssp. hololeucus in eastern Utah to give plants with white stems but glabrous involucres.

12. ssp. hololeucus (Gray) Hall & Clem. Includes the names gnaphalodes and zionis. Largely sympatric with ssp. consimilis, but intergradations between the two have not been observed.

13. ssp. iridis L. C. Anderson. Known from only two locations on barren gypsiferous shale.

13. ssp. junceus (Greene) Hall & Clem. Distinctive with fastigiate rushlike branches. Recently found in Mesa Co., CO (new for state), but not shown on map.

14. ssp. latisquameus (Gray) Hall & Clem. Very distinctive in southern part of range, but intergrades with ssp. graveolens in north-central New Mexico.

14. ssp. leiospermus (Gray) Hall & Clem. Includes names abbreviatus and oliganthus. Intergrades with ssp. mohavensis in Clark Co., NV.

15. ssp. mohavensis (Green) Hall & Clem. Includes name occidentalis. Closely related to ssp. consimilis.

15. ssp. nanus (Cronq.) Keck. Local, montane variant close to ssp. albicaulis.

16. ssp. nauseosus. Includes the names frigidus, pallidus, plattensis, pulcherrimus, and wyomingensis. A variable subspecies that seemingly intergrades only with ssp. albicaulis.

16. ssp. nitidus L. C. Anderson. A few pubescent-achened plants found in some populations. Distinctive with its yellowish-green stems (chartreuse) and very pleasant odor.

17. ssp. psilocarpus (Blake) L. C. Anderson. Very local glabrous-achened subspecies.

17. ssp. salicifolius (Rydb.) Hall & Clem. Distinctive with wide leaves; close to ssp. albicaulis but seems to mix a little with ssp. graveolens near Soldier Summit, UT.

17. ssp. texensis L. C. Anderson. Endemic to Guadalupe Mtns. of New Mexico and Texas with unusually short pappus.

18. ssp. turbinatus (Jones) Hall & Clem. Rarely has glabrous achenes but then distinct from ssp. bigelovii in villous corolla lobes and involucral features.

18. ssp. uintahensis L. C. Anderson. Apparently a local, stabilized hybrid involving C. parryi.

18. ssp. washoensis L. C. Anderson. Close to ssp. albicaulis but unique with white villous hairs distally on otherwise glabrous achenes.

19. C. paniculatus (Gray) Hall. Often easily identified by black bands on stems from insect or fungal attack.

C. parryi (Gray) Greene. Variation hardly accounted for with just trinomials; 11 subspecies:

20. ssp. affinis (Nels.) L. C. Anderson. Close to ssp. attenuatus, but involucres more stramineous.

20. ssp. asper (Greene) Hall & Clem. Distinctive with stalked glands but stalks sometimes fairly short.

21. ssp. attenuatus (Jones) Hall & Clem. Intermediate in range and morphology between ssp. howardii and ssp. nevadensis.

21. ssp. howardii (Parry) Hall & Clem. Includes name collinus. Geographically variable in plant height.

22. ssp. imulus Hall & Clem. Very local, perhaps only an extreme form of ssp. asper.

22. ssp. latior Hall & Clem. Distinctive with broadly oblanceolate leaves, looks like certain Haplopappus.

22. ssp. monocephalus (Nels. & Kenn.) Hall & Clem. High alpine form probably derived from ssp. nevadensis.

23. ssp. montanus L. C. Anderson. Known only from type locality and remote from near relatives.

23. ssp. nevadensis (Gray) Hall & Clem. Variable in stature and leaf size.

24. ssp. parryi. Wide ranging, hybridizes with C. nauseosus only at its range limits in Nevada and Wyoming.

24. ssp. salmonensis L. C. Anderson. Plants look much like C. nauseosus ssp. consimilis, but possibly derived from ssp. attenuatus.

24. ssp. vulcanicus (Greene) Hall & Clem. Plant form suggests some influence from C. nauseosus ssp. albicaulis.

C. pulchellus (Gray) Greene. Distinctive desert species with prominently angled achenes; 2 subspecies:

25. ssp. baileyi (Woot. & Standl.) Hall & Clem. Wide ranging, somewhat variable in involucral features.

25. ssp. pulchellus. Includes name elatior, which was applied to puberulent form (which grows intermixed with standard subspecies).

26. C. spathulatus L. C. Anderson. Only species in genus that rarely has a few ray flowers, but only in two geographically peripheral populations.

26. C. teretifolius (Dur. & Hilg.) Hall & Clem. Sometimes confused with C. paniculatus, this grows mostly on rocky slopes, whereas paniculatus grows in sandy washes.

27. C. vaseyi (Gray) Greene. Includes name bakeri. Looks somewhat like C. viscidiflorus but more closely related to C. depressus.

C. viscidiflorus (Hook.) Nutt. Most wide ranging and complex after C. nauseosus; five subspecies:

28. ssp. axillaris (Keck) L. C. Anderson. Confused with stenophyllus form of ssp. viscidiflorus but distinct.

29. ssp. lanceolatus (Nutt.) Hall & Clem. Includes names elegans, glaucus, latus, and spathulata; intergrades extensively with ssp. viscidiflorus.

30. ssp. planifolius L. C. Anderson. Local form with small heads and flat leaves.

30. ssp. puberulus (D. C. Eat.) Hall & Clem. Often with ssp. viscidiflorus but not intergrading.

31. ssp. viscidiflorus. Includes names latifolius, pumilus, stenophyllus, tortifolius, and varus. The combination C. v. ssp. viscidiflorus var. stenophyllus has already been made (Anderson 1980b); others will be made in upcoming monograph.

RANGE MAPS

The maps that follow (figures 1-31) depict the natural distribution of each taxon. More precise dot maps will be provided in the upcoming monograph. Ranges were determined from extensive field observations and from study of over 24,000 herbarium specimens.

ACKNOWLEDGMENT

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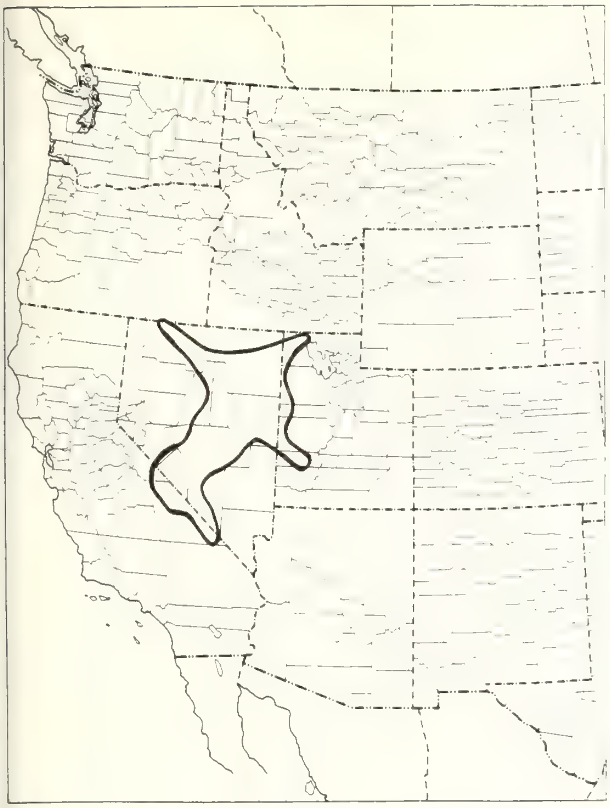

Figure 1.--Range of Chrysothamnus albidus.

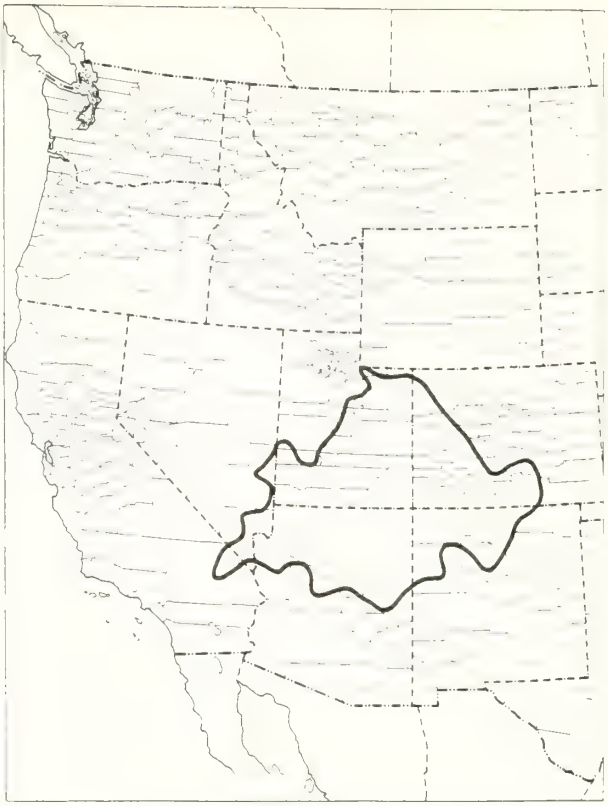

Figure 2.--Range of Chrysothamnus depressus.

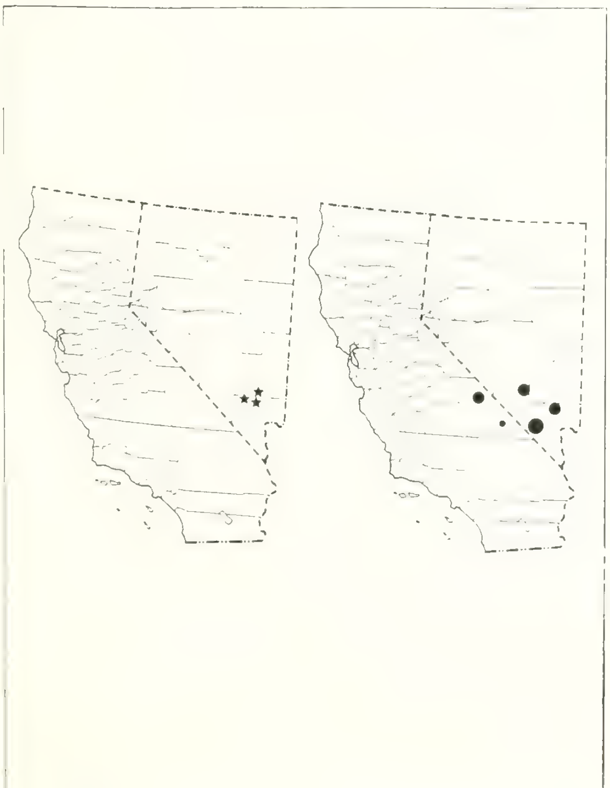

Figure 3.--Range of Chrysothamnus eremobius (stars); range of C. gramineus (dots).

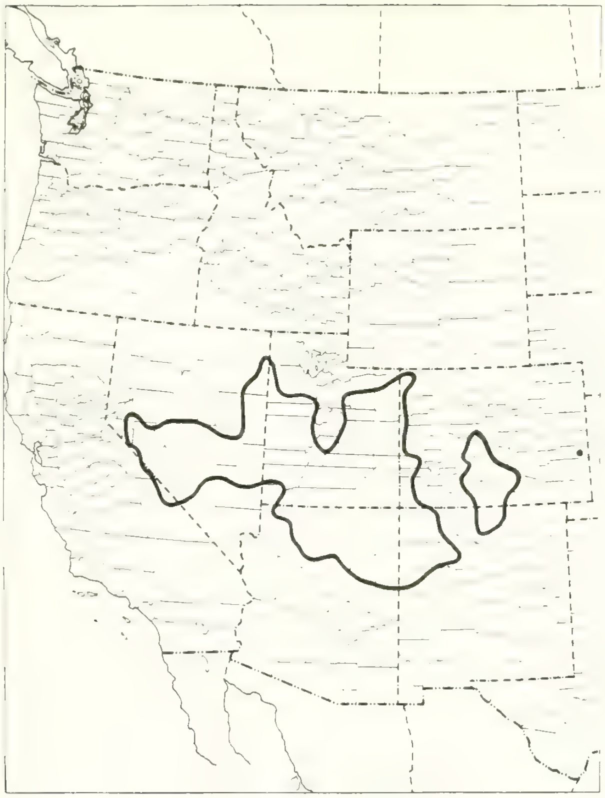

Figure 4.--Range of Chrysothamnus greenei.

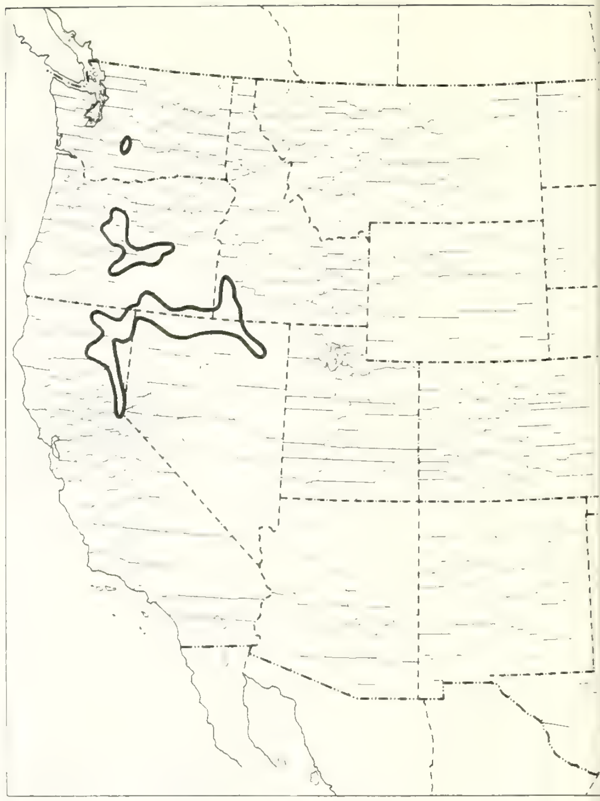

Figure 5.--Range of Chrysothamnus humilis.

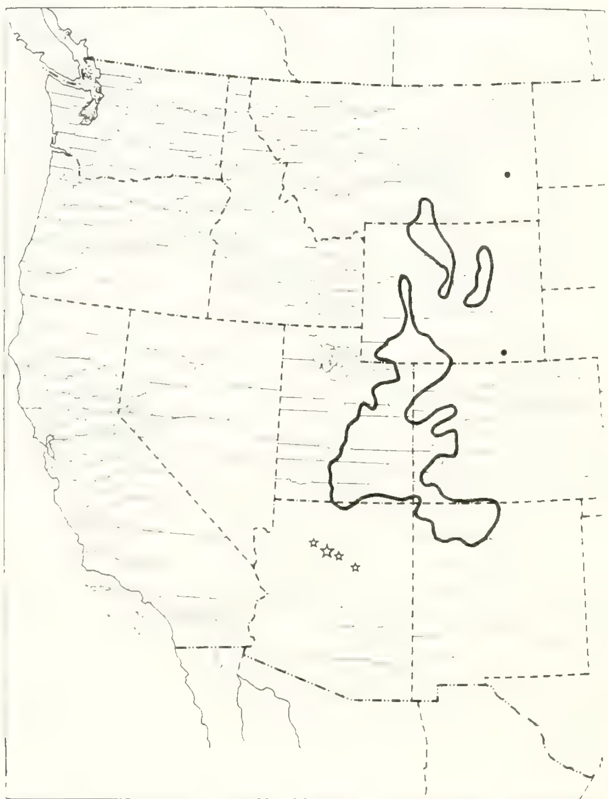

Figure 6.--Range of Chrysothamnus linifolius (dots and loops); range of C. molestus (stars).

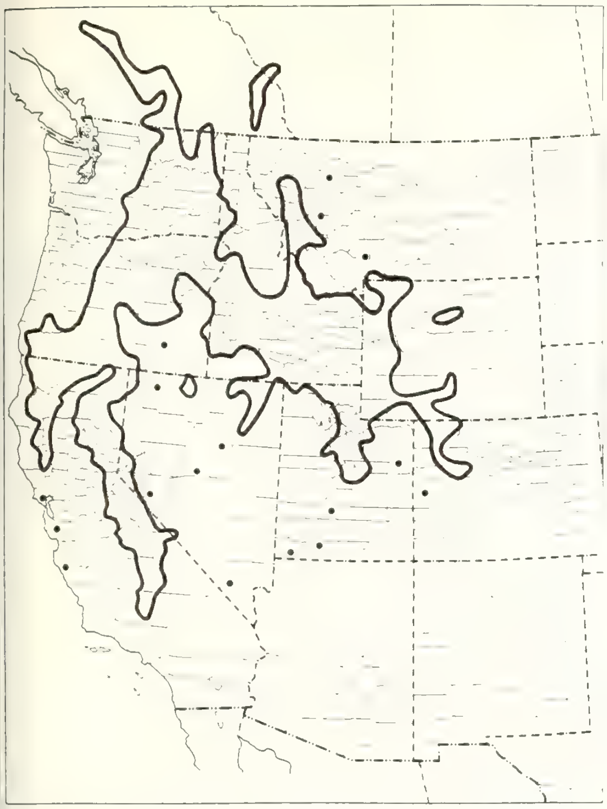

Figure 7.--Range of Chrysothamnus nauseosus ssp. albicaulis.

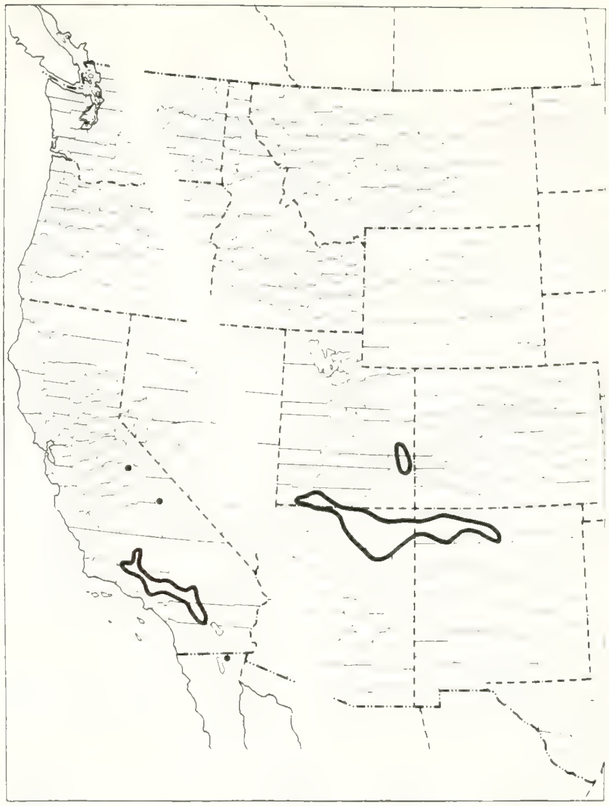

Figure 8.--Range of Chrysothamnus nauseosus ssp. arenarius (right map); range of C.n. ssp. bernardinus (left map).

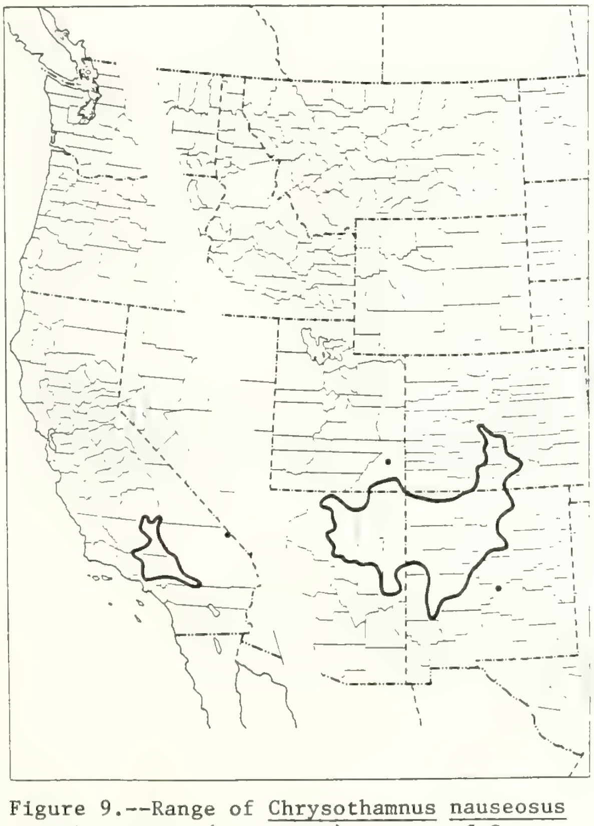

Figure 9.--Range of Chrysothamnus nauseosus ssp. bigelovii (right map); range of C.n. ssp. ceruminosus (left map).

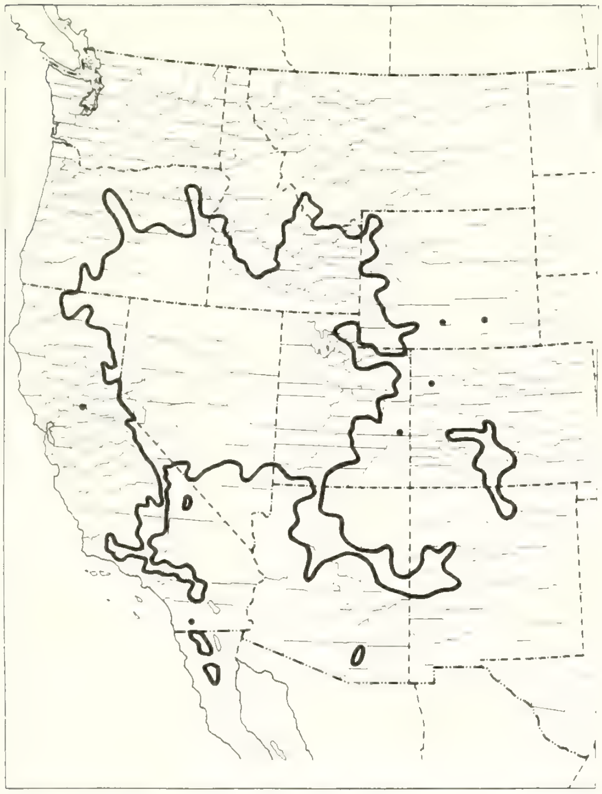

Figure 10.--Range of Chrysothamnus nauseosus ssp. consimilis.

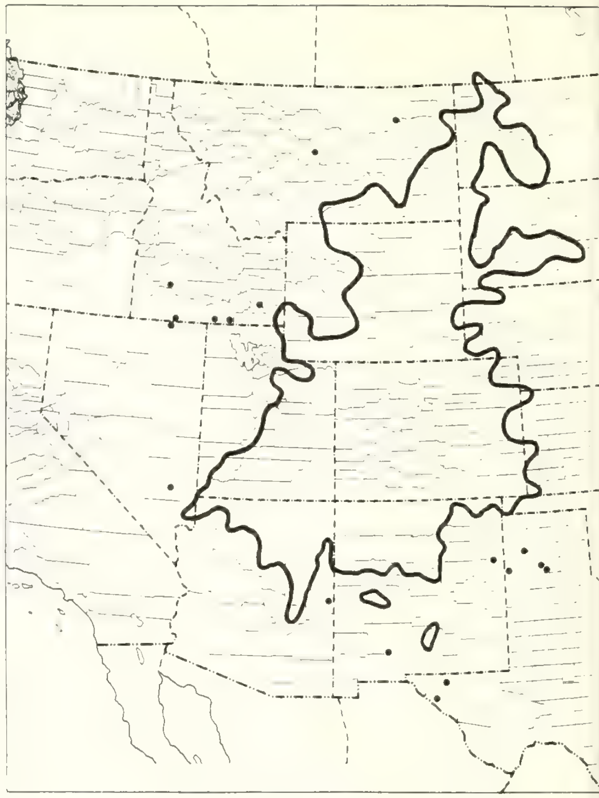

Figure 11.--Range of Chrysothamnus nauseosus ssp. graveolens.

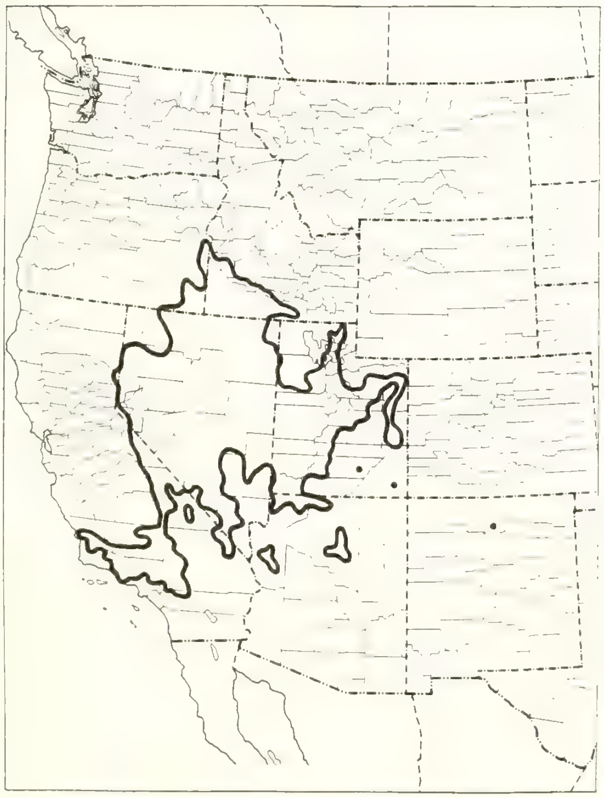

Figure 12.--Range of Chrysothamnus nauseosus ssp. hololeucus.

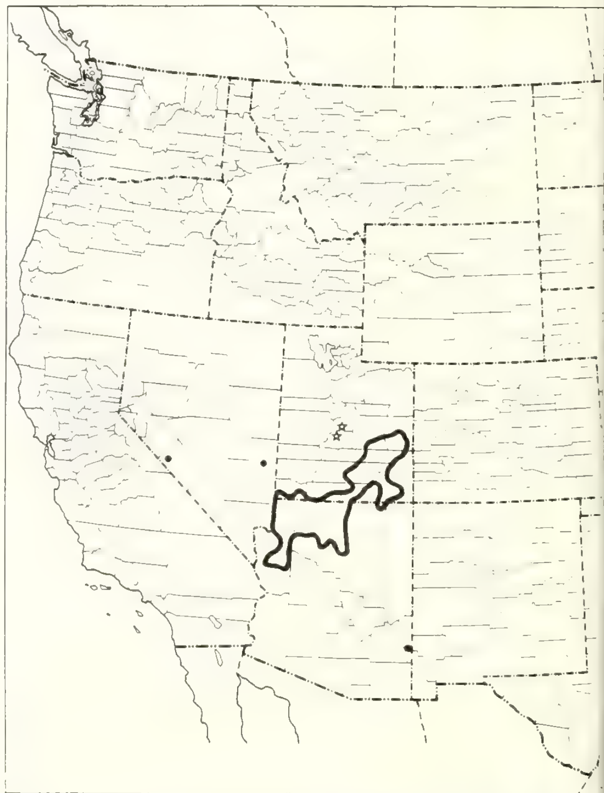

Figure 13.--Range of Chrysothamnus nauseosus ssp. iridis (stars); range of C.n. ssp. junceu (dots and loop).

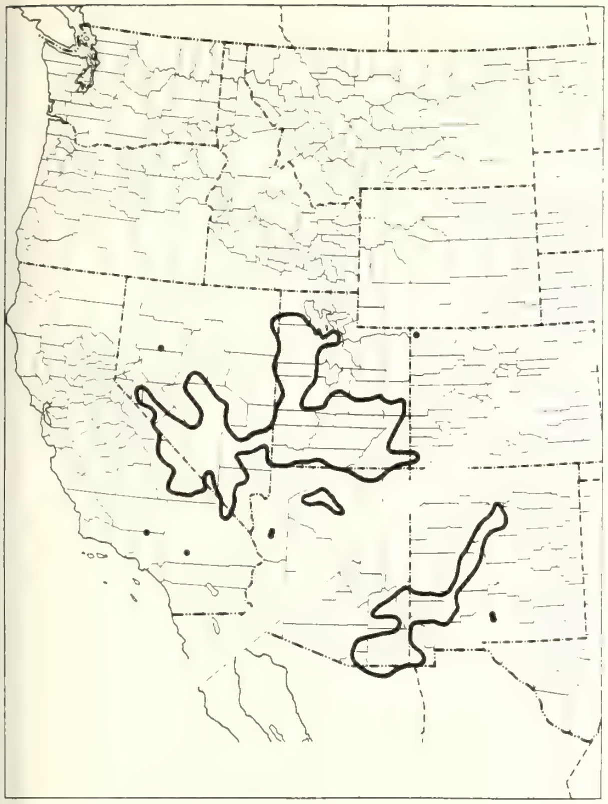

Figure 14.--Range of Chrysothamnus nauseosus ssp. latisquameus (lower right); range of C.n. ssp. leiospermus (upper left).

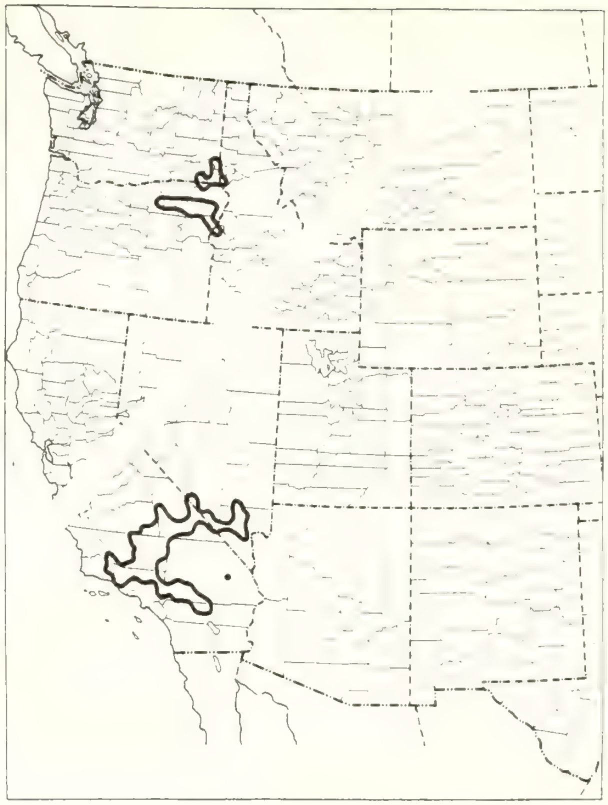

Figure 15.--Range of Chrysothamnus nauseosus ssp. mohavensis (lower map); range of C.n. ssp. nanus (upper map).

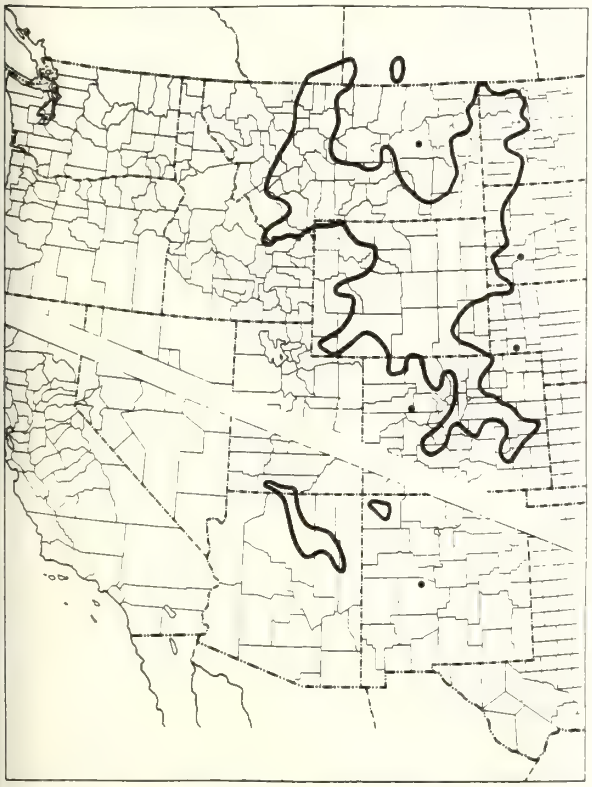

Figure 16.--Range of Chrysothamnus nauseosus ssp. nauseosus (upper right); range of C.n. ssp. nitidus (lower left).

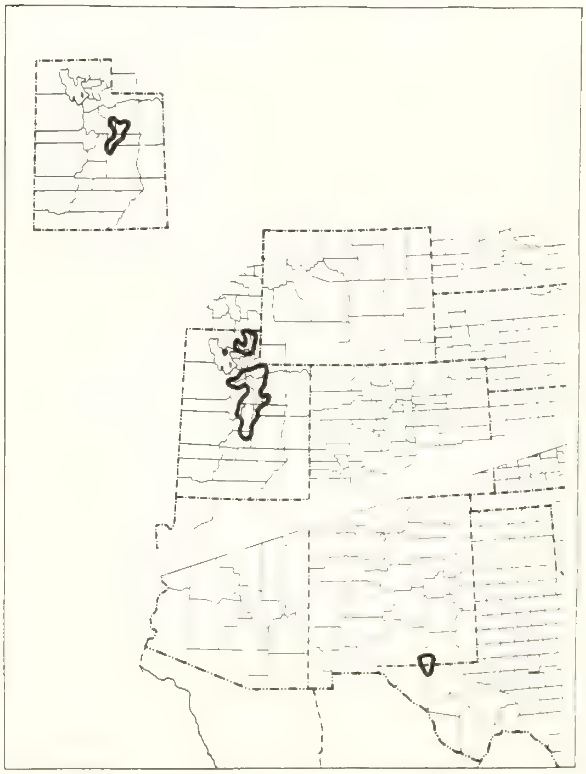

Figure 17.--Range of Chrysothamnus nauseosus ssp. psilocarpus (upper left); range of C.n. ssp. salicifolius (middle map); range of C.n. ssp. texensis (lower map).

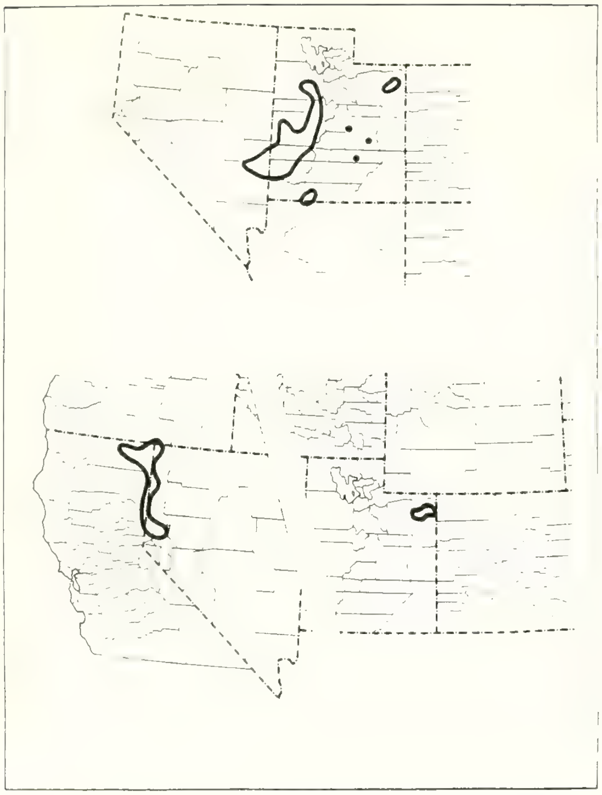

Figure 18.--Range of Chrysothamnus nauseosus ssp. turbinatus (upper map); range of C.n. ssp. uintahensis (lower right); range of C.n. ssp. washoensis (lower left).

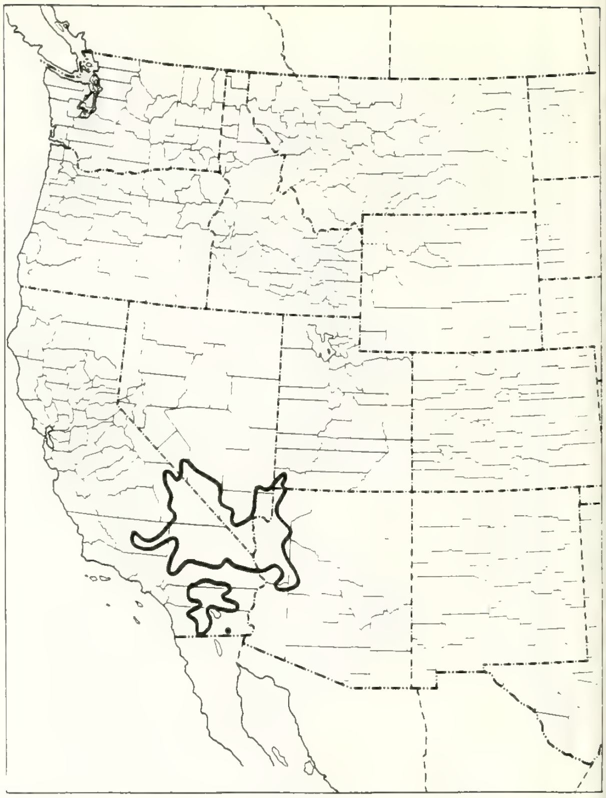

Figure 19.--Range of Chrysothamnus paniculatus.

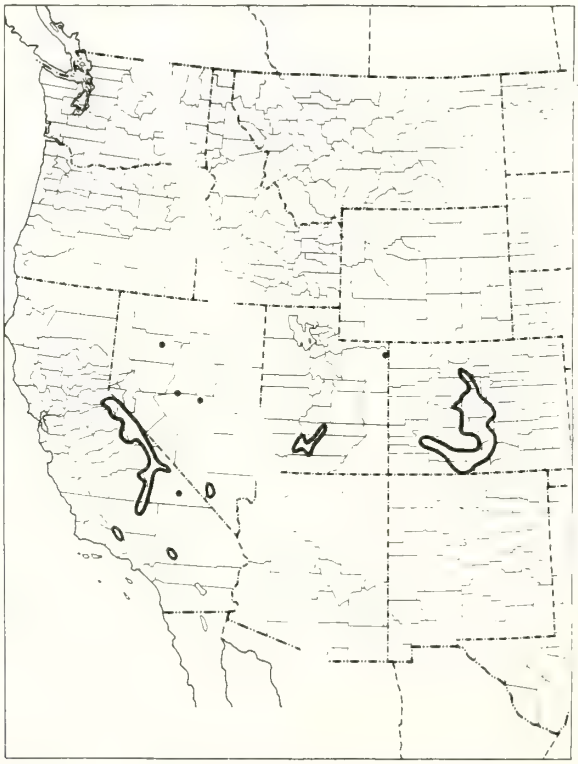

Figure 20.--Range of Chrysothamnus parryi ssp. affinis (right map); range of C.p. ssp. asper (left map).

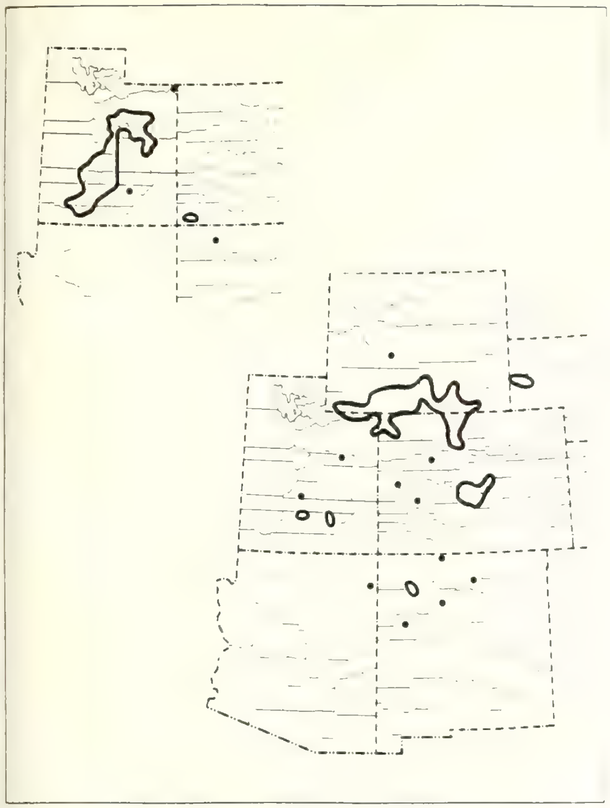

Figure 21.--Range of Chrysothamnus parryi ssp. attenuatus (upper left map); range of C.p. ssp. howardii (lower right map).

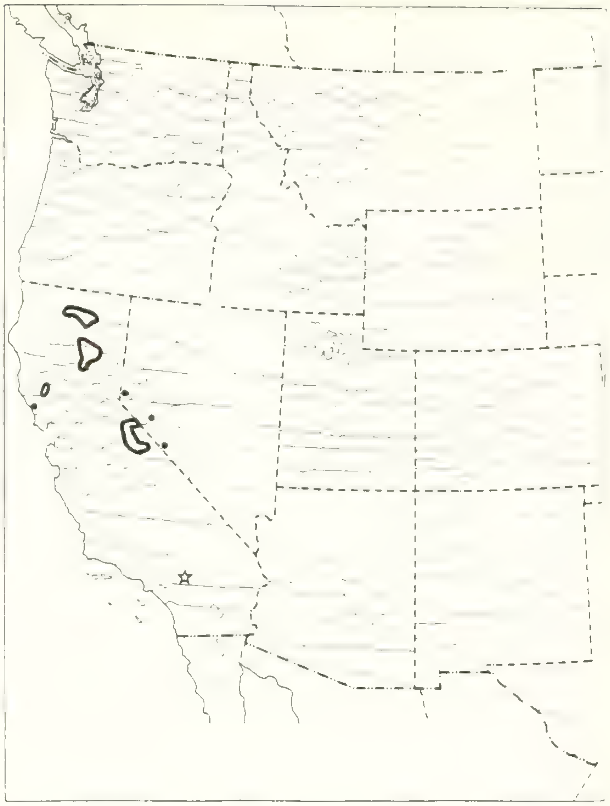

Figure 22.--Range of Chrysothamnus parryi ssp. imulus (star, lower map); range of C.p. ssp. latior (upper map); range of C.p. ssp. monocephalus (dots and loop, lower map).

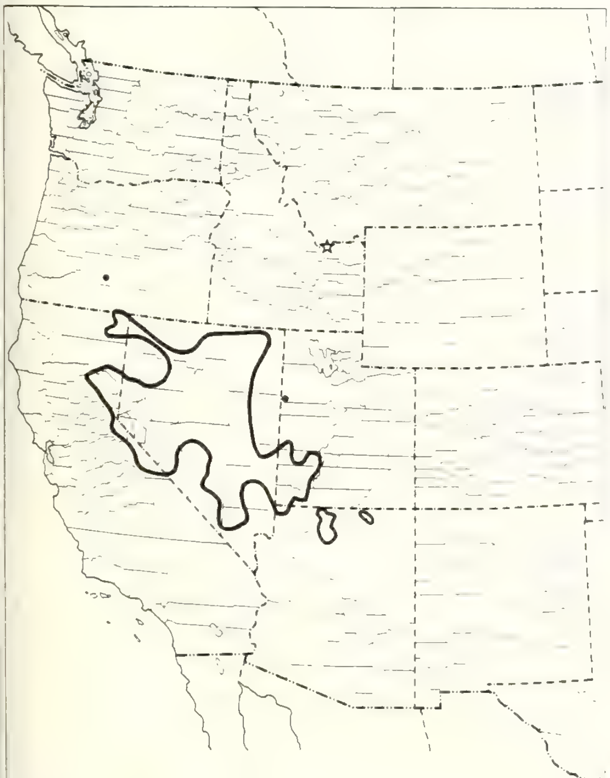

Figure 23.--Range of Chrysothamnus parryi ssp. montanus (star); range of C.p. ssp. nevadensis (dots and loops).

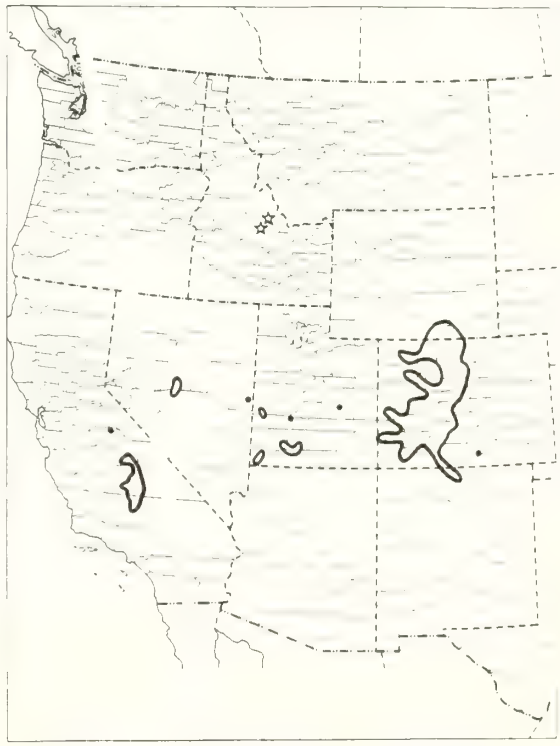

Figure 24.--Range of Chrysothamnus parryi ssp. parryi (dots and loops, right map); range of C.p. ssp. salmonensis (stars, right map); range of C.p. ssp. vulcanicus (left map).

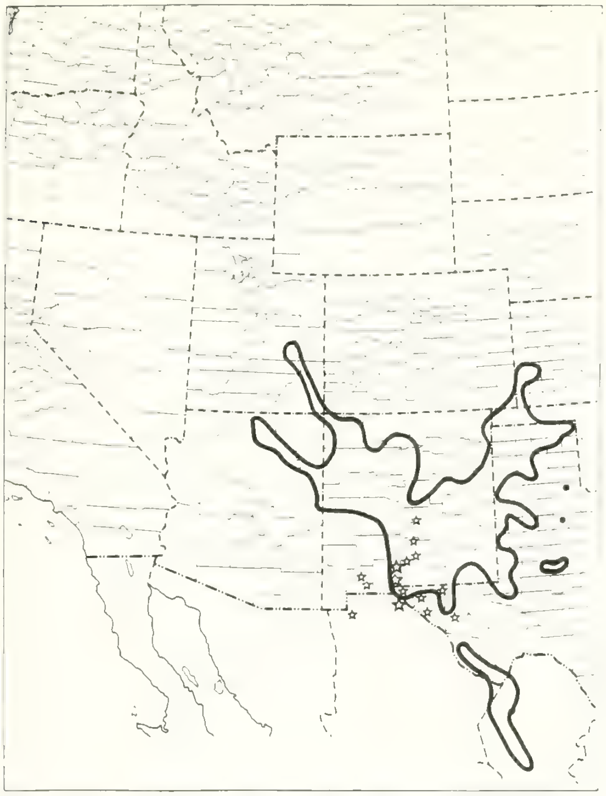

Figure 25.--Range of Chrysothamnus pulchellus ssp. baileyi (dots and loops); range of C.p. ssp. pulchellus (stars).

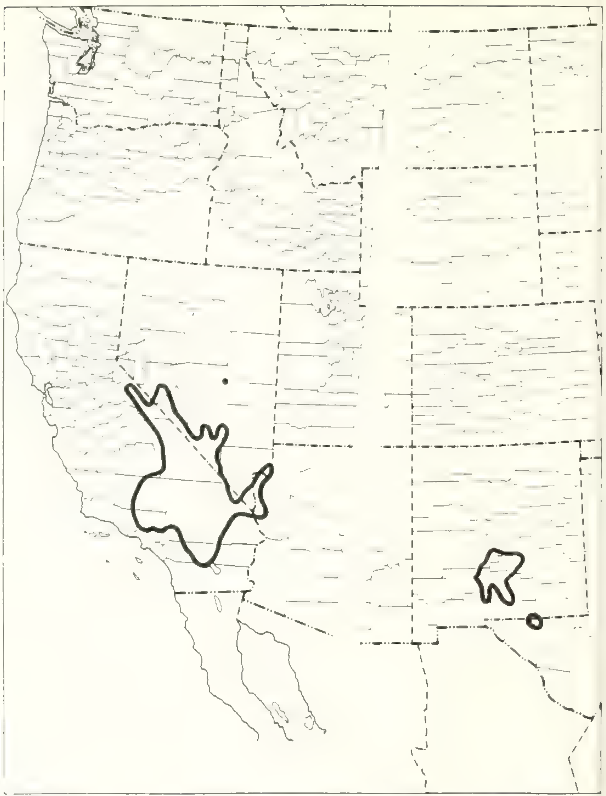

Figure 26.--Range of Chrysothamnus spathulatus (right map); range of C. teretifolius (left map).

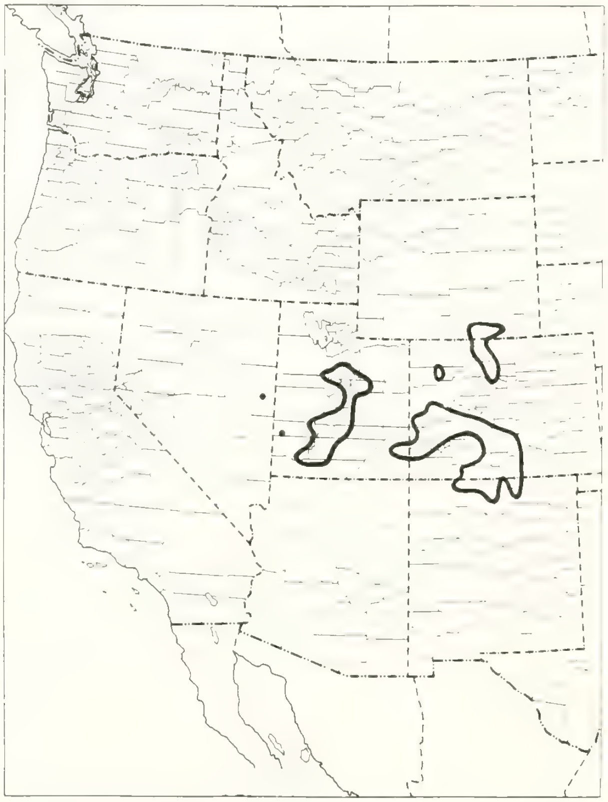

Figure 27.--Range of Chrysothamnus vaseyi.

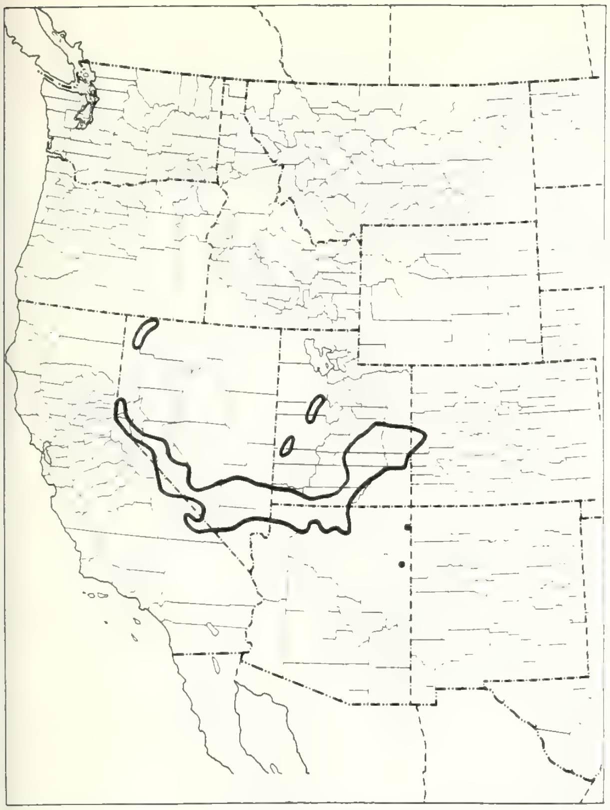

Figure 28.--Range of Chrysothamnus viscidiflorus ssp. axillaris.

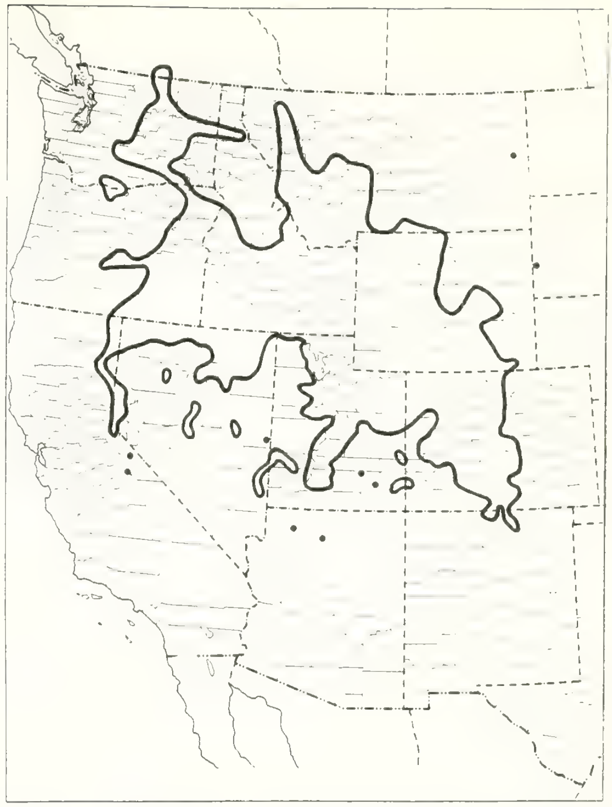

Figure 29.--Range of Chrysothamnus viscidiflorus ssp. lanceolatus.

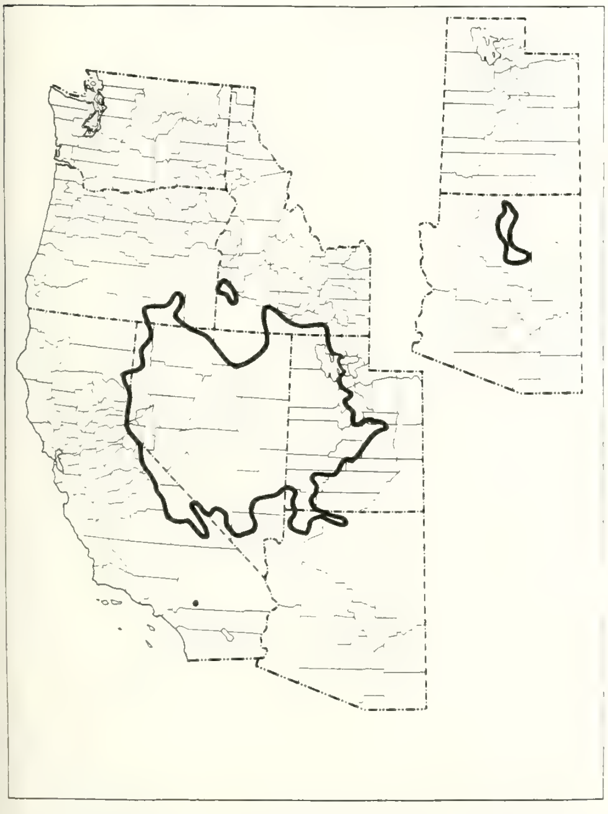

Figure 30.--Range of Chrysothamnus viscidiflorus ssp. planifolius (upper right map); range of C.v. ssp. puberulus (lower left map).

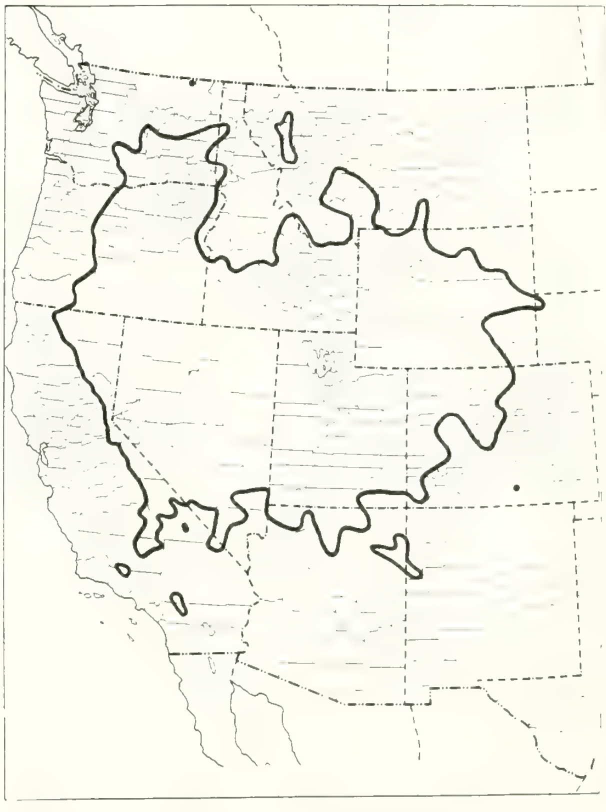

Figure 31.--Range of Chrysothamnus viscidiflorus ssp. viscidiflorus.

FRINGED SAGEBRUSH (ARTEMISIA FRIGIDA)--A NEGLECTED FORAGE SPECIES OF WESTERN RANGES

Allen Y. Cooperrider and James A. Bailey

ABSTRACT: Fringed sagebrush (Artemisia frigida) is widely distributed on western rangelands. While some consider it a pest species, many others consider it a valuable forage species. Data on food habits and forage preference of four wild ungulates on common range in southern Colorado suggest that it is preferred forage during all seasons except summer. The species spreads and reseeds itself well and has high resistance to grazing at the population level. Artemisia frigida has potential for use in grazing systems and in reseeding and rehabilitation. Range managers should be cautious about attempting to control or eradicate fringed sagebrush.

INTRODUCTION

Fringed sagebrush (Artemisia frigida) is one of the least understood shrubs and half-shrubs of the genus Artemisia in North America. In spite of increasing evidence of its great potential as a forage plant for livestock and big game, it continues to be studied very little. The species is so enigmatic that it seems to defy most traditional classifications. It is considered a forb by some researchers (Currie and others 1977) and a shrub by others (Dietz 1972). It is considered a pest species by some (Alley 1972), yet others report it to be a highly valuable forage species in areas as widely separated as Texas (Vines 1960), Montana (Spang 1954), and Mongolia (Anisimova and Ojun 1974). Furthermore, it seems to have physiological characteristics typical of both cool season and warm season plants (Williams and Markley 1973). Finally, although it is considered an increaser, invader, or indicator of overgrazing by many (Vines 1960; Sabo and others 1979), individual plants are quite susceptible to heavy grazing (Trlica and others 1977). In fact, populations of the species decrease or remain stable under certain grazing treatments (Jones 1965; Smith 1967).

This paper will review literature of the ecology, forage value, and response to grazing of fringed sagebrush, and suggest some explanations for the seemingly contradictory evidence in the literature. We will also discuss management and research implications of these explanations.

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ECOLOGY

Distribution

Fringed sagebrush is probably one of the most widely distributed and abundant species of its genus, with a range that extends from Mexico northward through most of the western United States and Canada into Alaska and from there to Siberia, Northern Asia, and Europe (Dayton 1937).

Habitat Sites

Fringed sagebrush is a common plant of the high plains along the eastern slope of the Rocky Mountains from Alberta and Saskatchewan south to northern New Mexico. It also occurs in the low semidesert valleys, mesas, and mountains of the Rocky Mountain and intermountain regions up to elevations of over 9,000 ft. (3 000 m) (Dayton 1937).

In the intermountain region, the species is dominant in dense stands along shallow depressions that collect moisture and floodwaters from summer rains. However, it also grows in lower density on slopes, foothills, and mountainsides intermixed with a variety of grasses, forbs, and shrubs (Dayton 1937).

The species occupies a fairly wide variety of sites, but grows most typically in full sunlight on dry, porous, coarse, gravelly, sandy, or shallow loam soils (Dayton 1937).

Growth and Reproduction

Growth of fringed sagebrush is not particularly rapid and it is not therefore considered an outstanding forage producer in terms of volume per plant. It typically does not grow over 24 inches (60 cm) high. Furthermore, grazing of individual plants results in decreased height growth (Trlica and others 1977; Savchenko 1973). This response is advantageous under moderate and heavy grazing pressure and thus, like other low-growing species such as blue grama (Bouteloua gracilis), fringed sagebrush has a selective advantage under heavy grazing pressure when growing in mixtures with taller grasses and forbs. The low growth form also

results in many plants being covered with snow and thus unavailable on winter ranges where taller shrubs are subjected to heavy browsing pressure from wild and domestic ungulates.

The most outstanding feature of fringed sagebrush is its tremendous reproductive potential. The species produces an abundance of very small seeds and can also multiply from rootstocks (Dayton 1937). Fringed sagebrush produces over 4 million seeds per pound, far in excess of most other rangeland plants (Plummer and others 1968). Early germination tests indicated that fringed sagebrush germinated poorly at first, but viability of seed increased for several years (Wilson 1931). Recent tests, however, have shown that high germination can be achieved under a wide range of temperatures, but that germination is affected greatly by water stress (Sabo and others 1979). In summary, fringed sagebrush appears to produce a large amount of seed that can germinate well under optimum conditions yet can also remain viable in the soil for many years until favorable conditions are present.

FORAGE VALUE

Evidence is strong that fringed sagebrush is one of the better shrubs on western ranges in terms of forage value. The evidence comes from several sources: food habits and forage preference of animals, nutritional analyses, and in vitro and in vivo digestion trails.

Wildlife

Many studies report fringed sagebrush is a major component of seasonal diets of wildlife species. Using fecal analysis, Bailey and Cooperrider (1982) found that fringed sagebrush was the single most important species in the winter diet of bighorn sheep (Ovis canadensis), pronghorn antelope (Antilocapra americana), mule deer (Odocoileus hemionus), and elk (Cervus canadensis), and was also important in the spring and fall diets for these same four species on Trickle Mountain in southern Colorado (table 1). This information supports previous observations on the value of fringed sagebrush to wild ungulates.

Blood (1967) and Sugden (1961), using feeding site examinations as well as rumen analyses, reported that fringed sagebrush made up 35 to 63 percent of the winter diet of California bighorn sheep in British Columbia and that it was actively sought out by bighorn sheep in midwinter. Todd (1972) noted that fringed sagebrush was one of the most common species in the diet of Rocky Mountain bighorn sheep.

Hoefs and Cowan (1979) report that fringed sagebrush was the second most abundant species in the annual diet of Dall sheep (Ovis dalli), the most abundant from December through April. They further state that most researchers agree that whenever fringed sagebrush is an important component in the vegetation cover of a sheep range, it is also an important forage species.

Table 1.--Percentage of fringed sagebrush (Artemisia frigida) in the diets of wild ungulates on common range on Trickle Mountain, CO, as determined by fecal analysis (Bailey and Cooperrider 1982)[1]

Season	Bighorn sheep	Pronghorn antelope	Mule deer	Elk
Winter	55	68	35	48
Spring	22	43	30	14
Summer	4	26	tr	5
Fall	20	24	11	7

[1]The fecal analysis technique is designed to determine food habits at the genus level; however, fringed sagebrush can be distinguished from other species in the genus. It was the only Artemisia species found in any great abundance on Trickle Mountain. Slide readers reported that virtually all of the sagebrush in winter fecal samples were fringed sagebrush. However, small amounts of other sagebrush species were found in fecal samples at other times of the year and are included in the percentages above.

Fringed sage, along with other sages (Artemisia spp.), has also been reported as a common species in diets of pronghorn antelope. More importantly, there is evidence that it is a preferred species, i.e., its consumption is disproportionate to its composition on the range (table 2). Mitchell (1980) reports substantial

Table 2.--Pronghorn antelope preference indices for fringed sagebrush in a rabbitbrush community in Saguache County, CO (derived from data in Bear and others 1973)

Season	Percentage of fringed sage in diet (D)	Percentage of fringed sage on range (R)	Preference Index (D/R)
April-June	37	2	18.5
July-September	3	3	1.0
October-March	23	4	5.8

use of fringed sagebrush and suggests that "the role and importance of Artemisia tridentata in the diet of pronghorns south of latitude 49°N. is assumed by A. cana and A. frigida in the annual diets of pronghorns in Alberta."

Similarly, fringed sage has been reported as a common species in the spring diet of mule deer in northern Colorado (Lucich 1977). Using fecal analysis he found that fringed sagebrush made up 64 percent of the diet in April, 16 percent in May, and then dropped sharply to less than 2 percent from June through September (table 3). Sugden (1961) reported that mule deer diet contained 63 percent fringed sagebrush on a range in British Columbia. Currie and others (1977) reported that tame mule deer selected 13 percent fringed sagebrush in April, 2 percent in May, 7 percent in June, and less than 1 percent from July through August on the Manitou Experimental Forest in central Colorado.

Thus, several major wild ungulate species in North America make considerable use of fringed sagebrush on ranges where it is present. Furthermore, evidence suggests that they actively seek the species. Bison (Bison bison) diets have been reported to contain over 20 percent of the species in March on heavily grazed shortgrass range in northern Colorado (Peden 1976). Mountain goats (Oreamnos americana) not only eat large quantities of it, but also appear to prefer it in winter where it is available (Adams 1981). The other major ungulates in North America, moose (Alces americana), caribou (Rangifer tarandus), white-tailed deer (Odocoileus virginiana), and muskox (Ovibos moschatus), probably do not make much use of it because their geographic distribution and habitat preferences are such that they do not occupy ranges where it is abundant.

Livestock

Studies also show that fringed sagebrush is highly palatable and nutritious for livestock. Dayton (1937) reported that the forage value of the species is highest in the Southwest where it rates fairly good in palatability for cattle and very good for sheep and goats, especially during the winter and spring. It is highly prized as sheep feed during the lambing season. He also reported that the species is considered practically worthless on the cattle ranges of the northern plains and prairies except during the late fall and winter. On the other hand, Macoun (1877), in early explorations of the Northwest, reported that fringed sagebrush was important winter feed for cattle throughout upper British Columbia and the dry Northwest, and that local stockmen often preferred it to

Table 3.--Percentage of fringed sagebrush in the diet of various North American wild and domestic ungulates by month and/or season

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Source
Cattle					20	23	0	4	9	--	9		Malechek (1966)
Cattle						2	1	5					Vavra and others (1977)
Domestic sheep		----60---											Spang (1954)
Bighorn sheep		-------55-------			-------22------			--------4--------			-------20--------		Bailey and Cooperrider (1982)
Pronghorn antelope		-------68-------			-------43------			-------26--------			-------24--------		Bailey and Cooperrider (1982)
Pronghorn antelope		-------23-------			-------37------			--------3--------			-------23--------		Bear and others (1973)
Mule deer		-------35-------			-------30------			--------tr-------			-------11--------		Bailey and Cooperrider (1982)
Mule deer					34	1	tr	tr	tr				Lucich (1977)
Elk		-------48-------			-------14------			--------5--------			--------7--------		Bailey and Cooperrider (1982)

cured grass or hay because it maintained livestock in "sleek and fat" condition even in the dead of winter.

More recent food habit studies tend to confirm the value of fringed sagebrush to livestock. Spang (1954) reported that the average diet of domestic sheep on a spring foothill range in Montana was 60 percent fringed sage in February and March on an area where the species was estimated to comprise less than 1 percent of the plant cover. Similarly, Malechek (1966) noted that the diet of cattle grazing native ponderosa pine/bunchgrass ranges on the Manitou Experimental Forest in Colorado consisted of up to 20 percent fringed sagebrush. Cattle diets on these ranges, however, contained less than 3 percent fringed sagebrush for the period from June through mid-August; the percentage rose to about 10 percent through December (table 3). In 1974 and 1975, Currie and others (1977) grazed the same areas with tame mule deer and found that they ate less fringed sagebrush than cattle although the seasonal pattern was similar (table 3). The techniques used may partly account for the lower utilization by mule deer. There is evidence that tame animals may select less fringed sagebrush. Schwartz and Nagy (1976) found that tame pronghorn ate significantly less fringed sagebrush than wild pronghorn from the same area. Vavra and others (1977) reported that esophageally fistulated cattle had a very low preference for fringed sagebrush during summer (table 3).

In summary, fringed sagebrush is not only important to wild ungulates, but also is a preferred species for domestic sheep and possibly even cattle during spring and fall. Evidence of the value of such forage for either wild or domestic ungulates does not appear to be an artifact of the technique used to estimate food habits; data are reported from studies using fecal analyses, rumen analyses, fistulated animals, feeding site examinations, range sampling, and tame animal observations.

Unfortunately, no comprehensive studies of nutritional value have been made. Proximate analyses of the species show that it has relatively high levels of crude protein (table 4). In fact, Anisimova and Ojun (1974) indicate it is one of the best protein sources for domestic sheep on Mongolian pasture lands, exceeding the major grass species of the region. However, numerous studies have shown that volatile oils in browse species, particularly conifers and members of the genus Artemisia, can reduce both palatability and digestibility of plants, making such analyses of limited value (Nagy and others 1964; Longhurst and others 1968). However, see Welch (1983) for a discussion that minimizes the importance of volatile oils in the digestive processes of animals that eat big sagebrush. Nutritional analyses that utilize in vivo or in vitro digestibility are better measures in that they can integrate such factors and thus provide a measure of how much actual energy or nutrients an animal can receive from the forage.

Table 4.--Proximate analysis of fringed sagebrush (from Anisimova and Ojun 1974)

Month/stage	Ash	CP	EE	CF	NFE
		Percent			
June: vegetative	17.4	21.3	2.4	24.6	34.3
July: floral shoots forming	7.4	11.9	3.2	32.3	45.2
September: full bloom	8.7	10.1	3.6	35.7	41.9
October: dormant	7.7	8.8	4.9	39.0	39.6

The few studies using such techniques suggest that fringed sagebrush is high in dry matter digestibility (DMD), digestible energy (DE), and digestible protein (DP). Dietz (1972) reported that DMD was 59.5 percent, which was higher than six other shrub species. Values for DE and DP reported by Taylor (1972) and Cook and others (1977) are somewhat inconsistent, but tend to be higher than those for other forages. Cook and others (1977) reported DE values for fringed sagebrush ranging from 2275 kcal/kg for winter to 3473 kcal/kg for spring. By comparison, the same authors report DE values for alfalfa ranging from 2336 kcal/kg in summer to 4312 kcal/kg in spring.

The overall evidence from food habits, preference indices, and nutritional analyses is that fringed sagebrush is a highly palatable, digestible, and nutritious forage that is preferred by many domestic and wild species during all seasons except summer.

RESPONSE TO GRAZING

The response of fringed sagebrush to grazing will be considered in terms of individual plant response and then in terms of population response.

Individual Plants

Trlica and others (1977) studied the effects of defoliation on individual fringed sagebrush plants by clipping 90 percent of the current annual growth during four phenological stages: quiescence (November 5-20), early growth (April 15-20), rapid growth (June 1-10), and near maturity (August 1-15) on the Central Plains Experimental Range in northern Colorado. All treatments resulted in significant reductions in seed stalk length, live crown coverage, and

herbage yield even after a minimum of 14 months of rest (table 5). Clipping was most detrimental during rapid growth (June).

Buwai and Trlica (1977) studied the effects of multiple defoliation of fringed sagebrush on the same area by clipping individual plants at two different intensities (60 and 90 percent of current annual growth removed) and at three phenological stages: quiescence (late October), rapid growth or flowers developing (early June), and near maturity (early August). All treatments resulted in reduction in live crown cover, plant height, live crown diameter, plant vigor, and herbage yield.

The limited evidence available suggests that individual plants are quite sensitive to grazing pressure and quite slow to recover.

Plant Populations

Sarvis (1923), Dayton (1937), and Klipple and Costello (1960) all reported that fringed sagebrush is considered an indicator of overgrazing on the northern Great Plains and in the northwestern United States and British Columbia. However, there is contradictory evidence from other areas and studies. Sarvis (1941), working on the northern Great Plains, reported that the species increased greatly during the first 10 years of heavy grazing but diminished in the next 15 years. After 25 years, density was similar to that on lightly grazed ranges. Demarchi and others (1968) noted that on the Bull River bighorn sheep winter range in British Columbia fringed sagebrush made up 8 percent of the cover of plant species on ranges with low accessibility to cattle whereas it was found in only trace amounts where accessibility was high. Jones (1965), on the other hand, reported that fringed sagebrush decreased significantly under winter elk grazing, but appeared to increase under summer cattle grazing. Johnson (1956) studied pastures that had been grazed from 1941 to 1950 on the Manitou Experimental Forest in southern Colorado at heavy, moderate, and light intensities, as well as not grazed. Grazing occurred from June 1 to October 31 each year. He noted that the percentage composition, number of plants per plot, and forage yield of fringed sagebrush increased, as grazing increased from light to heavy. However, all three measures were higher under no grazing than under light or moderate grazing. In one of the best documented, long-term studies of grazing impacts on ranges with sagebrush, Smith (1967) analyzed 18 years of data from the Manitou Experimental Forest, including some reported previously by Johnson (1956). He found that neither percentage cover nor percentage composition of fringed sagebrush was significantly affected by summer cattle grazing.

Perhaps the most enlightening study of fringed sagebrush is that of Savchenko (1973) who measured the age structure as well as the

Table 5.--Average seedstalk length, live crown cover, and herbage yield for plants of fringed sagebrush subjected to a singl defoliation. Measurements made in the fall after defoliated plants had received 14 to 26 months of rest (from Trlica and others 1977)

Phenological stage when defoliated	Seedstalk length	Livecrown cover	Herbag yield
	cm	percent	g/plan
Control	22	74	4.8
Quiescence	7	15	1.8
Early growth	5	9	1.0
Rapid growth	3	3	0.7
Near maturity	4	12	1.5

percentage of cover on areas subject to varying levels of grazing pressure from domestic sheep. His data indicate that increased grazing pressure resulted in an increased number of individual plants of fringed sagebrush, accompanied by a shift in the population structure to young plants rather than middle-aged or older ones (table 6). The maximum total cover as well as percentage of fringed sagebrush occurred at intermediate levels of grazing.

Whereas individual fringed sagebrush plants are quite sensitive to grazing pressure, populations are not. The study conducted by Savchenko (1973) suggests that under increased grazing pressure, populations of fringed sagebrush respond by producing more young plants.

DISCUSSION

The enigmatic character of fringed sagebrush may be examined by considering how it fits into the traditional dichotomy of decreaser versus increaser or invader species. In simplified form, decreasers are plants characterized by high palatability, limited ability to spread or reseed, and limited resistance to heavy selective grazing. Increasers, on the other hand, are less palatable, spread easily either by seed or vegetatively, and have a higher resistance to grazing. Invaders may be considered an extreme category of increasers. We will discuss each of these characteristics in relation to fringed sagebrush.

Table 6.--Age structure and percentage cover of fringed sagebrush populations on pastures subject to different intensities of grazing (from Savchenko 1973)

	Intensity of Grazing				
	Light	Moderate	Strong	Very Strong	Semi-denudation
Number of plants per plot by age class					
Young	4	8	13	20	79
Middle-aged	18	43	51	38	1
Old	18	9	8	18	1
Total	40	60	72	76	81
Percentage cover of fringed sagebrush	25	45	40	35	27
Total cover (all species)	40	60	60	50	30

Palatability

The evidence is strong that fringed sagebrush is a highly palatable, nutritious, and preferred shrub on most parts of its range during all seasons except summer for wild ungulates and domestic sheep. However, it is frequently stated that it is unpalatable and of little value to cattle in the Northwest and northern Great Plains.

Two hypotheses can be used to explain the apparent difference in forage value from region to region. First, the traditional explanation is that there is significant ecotypic or subspecific variation in the species with regard to palatability. Considering the great variation within big sagebrush (A. tridentata) that has been documented in the last 20 years (McArthur and Plummer 1978; McArthur 1979), and the substantial variation in palatability between big sagebrush subspecies, this theory deserves further investigation.

There is a second explanation, however, that does not require hypothesizing geographic or taxonomic variation. This is that fringed sagebrush is highly palatable relative to other forages during all seasons except summer, and that the evidence for lack of palatability is based on experience with summer cattle grazing. When one compares the percentage of fringed sagebrush in the diets of cattle reported by Vavra and others (1977) and Malechek (1966) with those of other wild and domestic ungulates (table 3), the pattern is not that different; cattle food habit data are simply not available for many ranges with fringed sagebrush for seasons other than summer.

Both theories are useful in that they can be easily tested. A systematic study of geographic variation in palatability, preference, and nutritional value of fringed sagebrush, combined with a taxonomic study, could determine the degree to which subspecific or ecotypic variation is responsible for any measurable geographic variation in forage quality. Similarly, year-round studies of food habits and forage preferences of cattle and sheep on fringed sagebrush ranges could determine the value of the species to livestock at times other than summer.

In any case, fringed sagebrush appears to be highly palatable at most times of year to most animal species, and in this respect is a typical decreaser species.

Establishment

Fringed sagebrush has a high ability to spread, reseed itself, and/or invade new areas. There is no evidence to contradict the assertion that the species may rapidly invade or increase on ranges heavily grazed by cattle in summer. The wide ecological amplitude of the species combined with its tremendous seed production and prolonged seed viability make it a formidable competitor on areas that have been opened up by

grazing or other disturbance. There is little question that fringed sagebrush behaves like an increaser or even an invader species.

Resistance to Grazing

At least some populations of fringed sagebrush appear able to remain stable or increase under heavy grazing pressure. On the other hand, individual plants are quite susceptible to heavy defoliation. The explanation appears to be in the population response shown by Savchenko (1973). The evolutionary "strategy" of fringed sagebrush appears to be to produce large amounts of viable seed rather than to develop resistance to grazing. Moderate to heavy grazing thus has the effect of shifting the age structure of the population to younger age classes without necessarily reducing the density of plants or the total cover. This type of density dependent increase in reproductive success has been reported and studied in many animal populations and is the basis for many wildlife management practices. Such a response has not been as well documented or studied in plant populations, and population dynamics approaches are not commonly utilized in range management in North America.

It is interesting to speculate as to the degree to which such a reproductive strategy is tied to seasonal unpalatability. Given that seedling establishment is a critical time period in the life history, one could predict that there would be tremendous selection for factors that would make seedlings unpalatable during their first few months; this selection pressure would be highest in plant species with a high reproductive rate. The role of volatile oils in reducing palatability and digestibility of plants has already been mentioned. Nagy (1966) noted that there were seasonal changes in volatile oil content of fringed sagebrush as well as big sagebrush and black sagebrush (A. nova), with the highest content in August and the lowest in April. A pattern like this would have the advantage of providing increased protection from grazing during the critical times when seed production is occurring, and when seedling establishment is at a peak.

In any case, the relative unpalatability of fringed sagebrush in summer confers a great advantage under a pattern of summer grazing by livestock and may explain the apparent inconsistencies in the literature. For example, the increase of fringed sagebrush under summer cattle grazing and decrease under winter elk grazing as reported by Jones (1965) could be explained by unpalatability during summer even in the absence of variation in preferences among animal species.

The overall pattern then is that fringed sagebrush is a species with high palatability (except during summer), good ability to spread and reseed, and high resistance to grazing at the population level. Such a species defies classification as either an increaser or decreaser, but seems to have the best characteristics of each. These properties make it a highly desirable species to have on the range except where summer forage is the primary factor limiting production of wildlife and/or livestock. On many western ranges, however, production of wildlife and livestock is primarily limited by the availability of quality forage at other times of year. Thus, fringed sagebrush may prove to be a far more valuable forage than is now recognized. It seems desirable to conduct research to test some of the conjectures of this paper and to develop optima grazing systems for ranges with fringed sagebrush for the benefit of both livestock and wildlife. The species would also appear to be likely candidate for reseeding in many areas, although Plummer and others (1968) do not give it a particularly good overall rating for reseeding suitability for Utah.

The evidence presented here also suggests that range managers should be cautious about embarking on programs aimed at eradicating the species, as proposed by Alley (1972). First, control may be difficult due to the high rate o seed production and prolonged viability of seed. Second, drastic reduction in the density of the species may be quite detrimental to wild ungulates in an area if they are relying on fringed sagebrush for fall, winter, or spring forage. Third, if field managers increased spring or fall livestock grazing, there may be opportunities for utilizing rather than eradicating the resource. Finally, if range manager determine that eradication or reduction of fringed sagebrush is desirable, they should consider whether it might be easier and cheaper to do so through the use of sheep, goats, or other ungulate species through fall and/or winter grazing rather than embarking on an expensive program of herbicide application and/or mechanical control followed by reseeding

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ARTEMISIA TRIDENTATA SSP. SPICIFORMIS: DISTRIBUTION AND TAXONOMIC PLACEMENT

E. Durant McArthur and Sherel K. Goodrich

ABSTRACT: Subalpine big sagebrush (Artemisia tridentata ssp. spiciformis) is widely distributed and occurs in large uniform stands in several areas. It is probably a stabilized hybrid from A. tridentata ssp. vaseyana and A. cana ssp. viscidula parental stock. Several large populations (up to 750 acres [about 300 ha] in size) are mapped.

INTRODUCTION

Subalpine big sagebrush (Artemisia tridentata Nutt. ssp. spiciformis [Osterhout] Goodrich & McArthur) is found in mountains of central and north-central Colorado, west-central Wyoming, southeastern Idaho, and central and north-central Utah (fig. 1). In Utah these plants have been referred to as A. rothrockii A. Gray. Both Ward (1953) and Shultz (1983) maintained that A. rothrockii is restricted to California. The Utah materials are clearly referable to the type specimen of A. spiciformis which taxon was named and described by Osterhout (1900) from materials collected in North Park, CO.

In the original description of A. spiciformis, Osterhout (1900) described the plants as having the heads of A. cana Pursh and the leaves of A. tridentata. To this comparison we add: with the sprouting feature and the small, multistemmed habit of A. cana ssp. viscidula, but forming communities on upland montane, well-drained sites; sites similar to those occupied by A. tridentata ssp. vaseyana (Rydb.) Beetle.

Beetle (1959) made the combination Artemisia tridentata ssp. vaseyana forma spiciformis. However, with the head size, sprouting feature, and growth form of A. cana, we feel the plants are too closely aligned with A. cana, or at least too different from A. tridentata ssp. vaseyana to be

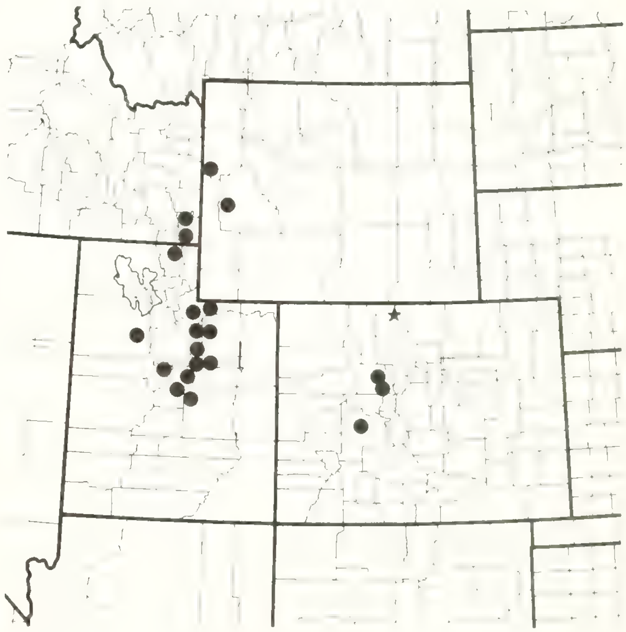

Figure 1.--Dot map distribution of populations of subalpine big sagebrush (A. tridentata ssp. spiciformis). Locations are from Goodrich and others (1985). Star is type location.

considered a form of that taxon. In addition, the size of the heads and number of flowers per head are more like those of A. cana than something intermediate between A. cana and A. tridentata. We feel that plants of A. tridentata ssp. spiciformis exhibit a unique set of features and represent a distinct taxon that is more sharply defined than several other sagebrush taxa.

Teeth or lobes on persistent leaves are the most obvious and about the only morphological features by which A. cana and A. tridentata are distinguished in taxonomic works. Based on this feature and the habitat, we have placed A. spiciformis as a subspecies of A. tridentata (Goodrich and others 1985).

Implications of a hybrid origin (involving A. cana and A. tridentata) are strong. However, we feel these plants represent a taxon as distinctive as many other Artemisia taxa. Other recognized Artemisia taxa are also thought to be of hybrid

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origin. For example, A. tridentata ssp. wyomingensis has been suggested to have been derived from A. tridentata ssp. vaseyana x A. tridentata ssp. tridentata or A. tridentata ssp. x A. nova (Beetle and Young 1965; McArthur 1983); A. rothrockii (in the narrow California sense) has been suggested to have been derived from A. arbuscula x A. tridentata (Ward 1953.)

The purpose of this paper is to supplement our formal recognition of A. tridentata ssp. spiciformis (Goodrich and others 1985) by documenting the occurrence of large uniform populations of this taxon. And, to locate the A. tridentata ssp. vaseyana and A. cana ssp. viscidula plants nearest each population. One concept of the taxon is that of an incidental hybrid of limited significance (Shultz 1983).

POPULATIONS OF SUBALPINE SAGEBRUSH

The subspecies occurs in the mountains of several western states (fig. 1). The populations listed in table 1 are free of one or both putative parents. Each population is mapped (fig. 2). We believe the size and the number of these large populations are compelling evidence that the plants are self sustaining and the taxon valid.

There are other populations that bear on the question of the independence of the taxon. A population, probably less than 5 acres (2 ha) in size, on the Stansbury Mountains, Tooele County, UT (Tye 1259, BRY)[1] is adjacent to populations of A. tridentata ssp. vaseyana but is separated by nearly 50 miles (80 km) from the nearest known population of A. cana.

Other smaller populations of subalpine sagebrush include some in Colorado on the Eagle River near Minturn (Osterhout 3370 and 3384, RM; McArthur 1428 and 1431, SSLP) and at North Park--the type location (Osterhout 2011 and 2255, RM; McArthur 1434, SSLP). Although these populations are smaller, they are, nevertheless, composed of distinctive ssp. spiciformis plants. Plants in these Colorado populations are adjacent to A. tridentata ssp. vaseyana plants, but further removed from A. cana ssp. viscidula plants. The ssp. spiciformis plants in these locations showed no visible evidence of introgression with either putative parent.

ACKNOWLEDGMENT

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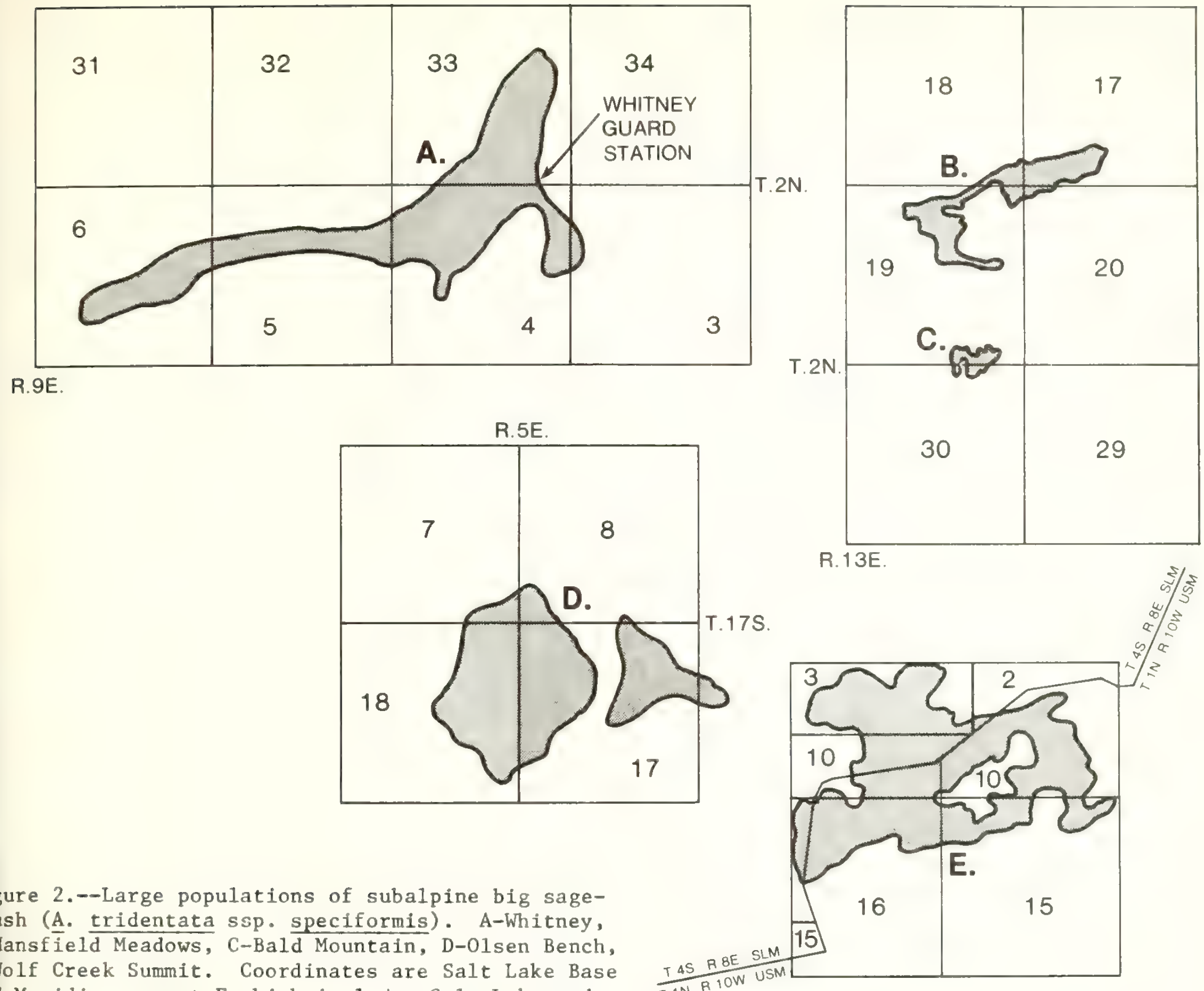
Table 1.--Some large Utah populations of subalpine big sagebrush (A. tridentata ssp. spiciformis)

Population	Approximate size[1]	Elevation[1]	Approximate distance from populations of: A. cana ssp. viscidula	Approximate distance from populations of: A. tridentata ssp. vaseyana
	Acres	Feet		
Wolf Creek Summit[2], Wasatch Co.	750	9,300	2 miles[1]	Adjacent to
Whitney, Summit Co.	550	9,300	Near at the lower end but wholly free for the length of the population (ca. 3 miles)	Adjacent to the lower end but free for 2 miles at the upper end.
Mansfield Meadows[3], Summit Co.	135	10,500	1 mile	1 mile
Bald Mountain Summit Co.	25	10,600	2 miles	2 miles
Olsen Bench[3], Sanpete Co.	500	10,400	4 miles	1 mile

[1]Conversions: acre = 0.405 ha; ft = 0.305 m, mi = 1.61 km.
[2]Isolated from A. cana by conifer and aspen forest.
[3]Isolated from both A. cana and A. tridentata ssp. vaseyana by conifer forest.

[1]Collection number and herbarium of deposit. Herbaria abbreviations: BRY = Brigham Young University, RM = University of Wyoming, SSLP = Shrub Sciences Laboratory.



igure 2.--Large populations of subalpine big sage-rush (A. tridentata ssp. speciformis). A-Whitney, -Mansfield Meadows, C-Bald Mountain, D-Olsen Bench, -Wolf Creek Summit. Coordinates are Salt Lake Base nd Meridian except E which includes Salt Lake and intah meridians. Map D is adapted from Ellison 1954). All other maps are original. Authors isited all populations.

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HABITAT RELATIONSHIPS OF SANDSAGE (ARTEMISIA FILIFOLIA) IN SOUTHERN UTAH

Lars L. Rasmussen and Jack D. Brotherson

ABSTRACT: Ten populations of sandsage in Washington County, UT, were paired with 10 adjacent populations for comparison studies of vegetation and soil nutrient components. Perennial grasses and forbs were much more abundant in the sandsage communities than in the adjacent desert types, although species diversity was lower. Several species were common to both types. With the exception of copper, soil nutrients were significantly lower on the sandsage sites. Indications are that sandsage has adapted to habitats of low fertility. This did not appear to affect the nutrient quality of sandsage as its nutrient content was found to be comparable to other shrubs.

INTRODUCTION

Sandsage (*Artemisia filifolia* Torr.) is likely the most widespread shrub species occurring on sand dunes and sandhills (McArthur and others 1979) in the southern Black Hills of South Dakota, Wyoming, Colorado, Nebraska, Kansas, Texas, Utah, Arizona, and Nevada (McKean 1976). Despite its widespread distribution, little research has been published concerning this species. Recent research has concerned landscape potential and propagation (Tipton and McWilliams 1976 and 1977), physiology (Hoehne and others 1968; Torrance and Steelink 1974), eradication (McIllvain and Armstrong 1963; Scifres and Polk 1974), and faunal associates (Cannon and Knopf 1981; Miller and Kevan 1979).

There is a lack of information concerning the ecology of sandsage. The purpose of this study is to describe the habitat and ecological relationships of selected sandsage populations in comparison to adjacent vegetation types in southern Utah.

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STUDY AREA

Sandsage communities in Washington County (fig. 1) are generally associated with deep sand deposits. These deposits are formed by the weathering of Navajo, and possibly Kayenta, sandstone formations.

Sandsage is the dominant overstory component within its community. The understory is composed primarily of annuals with a few sand-loving perennial forbs and grasses. Adjacent vegetative communities vary, but they are predominantly blackbrush stands associated with shallow coarse soils (Callison 1983).

The climate of the study area is characterized by mild winters and hot summers. Average annual temperatures range from 58° to 66 °F (14° to 19° C) with a frost-free period of 190 to 205 days. Most precipitation occurs in the form of rain and averages 8 to 10 inches (200 to 275 mm) annually. Precipitation falls primarily as gentle showers in winter and early spring, and as intense thunderstorms during July and August (Mortensen and others 1977).

METHODS

Ten populations of sandsage in Washington County, UT, were selected for study in June and July of 1984. Sites were selected that represented a cross section of conditions within the sandsage populations in the county. Sandsage sites were paired with sites in adjacent vegetation zones to help define the habitat requirements of sandsage.

Thirty-three (1-m^2) quadrats were stratified across each site in three 36-yard (33-m) parallel transects. Each quadrat was divided in fourths creating 132 quadrats per site. Total living cover was estimated in each quadrat. Frequency data from the quadrats were collected for exposed rock, bare soil, litter, cryptogams, trees, shrubs, perennial grass, annual grass, perennial forbs, annual forbs, and individual plant species.

Three soil samples were taken along each transect line at 33-foot (10-m) intervals from the top 8 inches (20 cm) of soil and later combined for laboratory analyses. This depth is considered adequate based on Ludwig's results

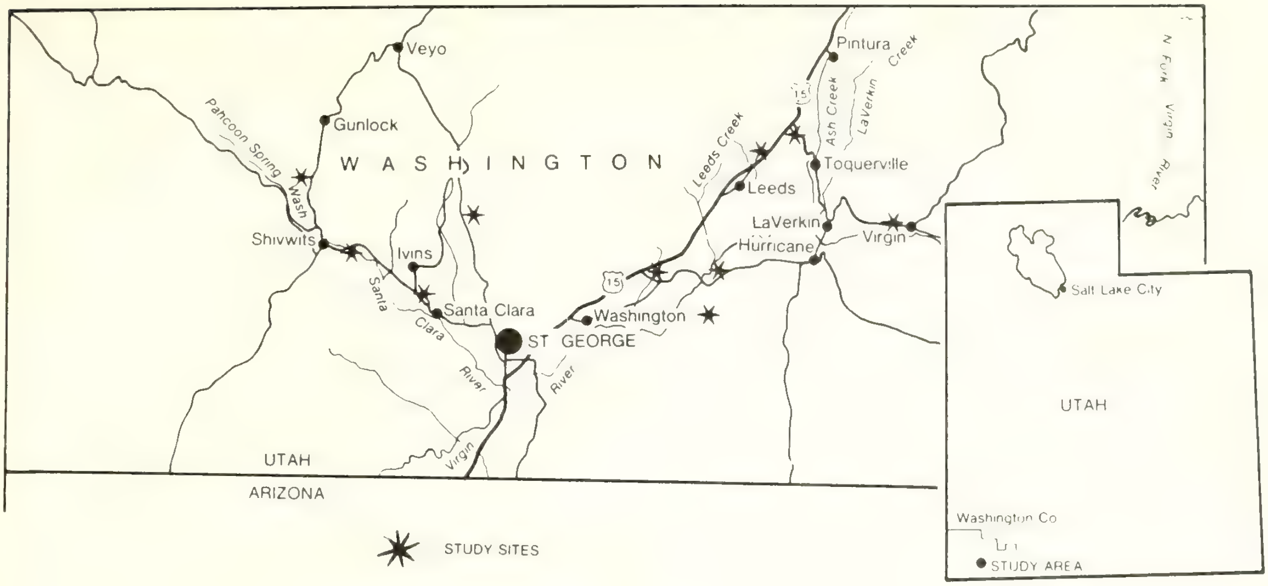

Figure 1.--Map of study site locations in Washington County, UT.

(1969) which show that the surface decimeter of soil yields 80 percent of the information useful in correlating plant response with concentrations of essential mineral nutrients in the soil. Supporting these results, Holmgren and Brewster (1972) show that greater than 50 percent of the fine roots of plants in desert communities are found in the top 6 inches (15 cm) of the soil profile.

Soil samples were analyzed for texture (Bouyoucos 1951), pH, soluble salts, cation exchange capacity, mineral composition, and organic matter. Soil pH was determined with a glass electrode pH meter. Soluble salts were determined with a Beckman electrical conductivity bridge. Exchangeable calcium, magnesium, potassium, and sodium were extracted with DTPA (diethylene triamine-penta-acetic acid (Lindsay and Norvell 1969). A Perkin Elmer Model 403 atomic absorption spectrophotometer was used to determine individual ion concentrations (Isaac and Kerber 1971). Phosphorus was extracted with sodium bicarbonate (Olsen and others 1954). Organic matter was estimated from total carbon using methods described by Allison (1965).

Cluster analysis based on Ruzicka's (1958) similarity index was used to group sandsage and adjacent communities. Individual species were also clustered on niche overlap values related to their geographical distribution patterns (Cowell and Futuyma 1971). Means and standard deviations were computed for all biotic and abiotic variables measured. Prevalent species were selected from frequency values using a procedure described by Warner and Harper (1972). Diversity indices were computed using the Shannon-Weaver index (Shannon and Weaver 1949). Interspecific association patterns were computed using Cole's (1949) index.

RESULTS AND DISCUSSION

Sandsage in southern Utah occupies aeolean deposits of sandy soil formed primarily by weathering of Navajo sandstone. There were several differences in edaphic factors in the sandsage and adjacent communities (table 1). Exposed rock and soil gravel levels were significantly higher on the adjacent sites. The sandsage soils had significantly less clay and organic matter than the adjacent site soils. With the exception of copper, nutrients were also less abundant in soils occupied by sandsage. The lower soil fertility of the sandsage habitat also resulted in a significantly lower cation exchange capacity. Tisdale and Nelson (1975) stated that soils with greater amounts of clay and organic matter generally have higher exchange capacities than more sandy soils. We found that where cation exchange capacities were low, percent clay and percent organic matter were also low. These results may indicate that sandsage is adapted to less fertile soils than are the species of adjacent communities. Possible explanations for sandsage survival in such areas include reduced mineral requirements for growth, increased ion exchange capacity of the root system, or the ability of sandsage to concentrate nutrients in its tissues to acceptable levels for growth.

Our data (table 2) indicate that sandsage accumulates mineral nutrients well above levels found in the soils in which it grows. Concentration ratios (plant/soil) ranged from a low of 5:9 for sodium to 484.2 for potassium. The high concentration ratios for potassium (484.2) and phosphorus (342.5) are not well understood. When the mineral content of sandsage tissue was compared with the mineral content of several other desert shrubs, the values were equivalent

Table 1.--Means ($\bar{x}$) and standard deviations (SD) for soil factors and significance levels for the difference of the means observed in sandsage and adjacent communities in Washington County, UT. Significance levels were computed using the Student's t-statistic

Soil factor	Sandsage X	Sandsage SD	Adjacent X	Adjacent SD
Bare soil %	94.0	4.9	80.8	27.2
Exposed rock %	5.5	8.0	53.0	31.0
Sand %	86.1	16.5	78.3	8.94
Silt %	7.7	16.4	11.47	0.58
Clay % ***[1]	4.12	1.09	9.73	5.42
Organic Matter % **	0.152	0.102	.305	0.138
pH	7.59	0.33	7.71	0.26
Soluble salts (ppm)	0.551	0.620	0.71	0.68
CEC (meq/100g) ***	4.76	3.61	10.13	4.17
Calcium (ppm) *	1128	1595	4720	7140
Magnesium (ppm) *	58.2	34.1	204	163
Sodium (ppm)	8.00	3.47	8.85	3.48
Potassium (ppm)	49.9	18.5	168.4	84.6
Iron (ppm)	9.16	9.14	12.5	11.6
Manganese (ppm)	4.55	3.2	8.24	8.11
Zinc (ppm)	0.433	0.220	0.377	0.194
Copper (ppm) **	0.195	0.580	0.0672	0.414
Phosphorus (ppm)	7.598	0.328	7.712	0.263

[1]Significance levels: * = 0.1; ** = 0.01; *** = 0.005.

Table 2.--Means and standard deviations (SD) for mineral nutrient concentrations in sandsage soils and sandsage tissue along with ratios of plant to soil concentrations

Nutrient	Mean soil concentrations	Mean plant concentrations	Plant/soil ratios
Calcium (ppm)	1128.00	7971.00	7.06
SD	±1595.00	±995.00	
Magnesium (ppm)	58.20	1874.00	32.19
SD	±34.10	±221.10	
Sodium (ppm)	8.00	47.70	5.96
SD	±3.50	5.85	
Potassium (ppm)	49.90	24,160.00	484.16
SD	±18.50	3,052.90	
Iron (ppm)	9.20	92.60	10.06
SD	±9.10	±29.80	
Manganese (ppm)	4.60	30.43	6.61
SD	±3.20	±9.55	
Zinc (ppm)	.43	23.80	55.34
SD	±.22	±3.37	
Copper (ppm)	.20	11.65	58.25
SD	±.58	±2.78	
Phosphorus (ppm)	7.60	2603.00	342.5
SD	±.33	±236.59	
Nitrogen (%)	.17	2.38	13.94
SD	±.07	±0.28	

(Fairchild and Brotherson 1980) and therefore would support the hypothesis that sandsage (in Washington County, at least) is adapted to soils of lowered fertility.

Forty-eight species were encountered in the sandsage communities, while 72 species were encountered in the adjacent communities. The large number of species on the adjacent sites was due to the variability in community types found adjacent to the sandsage communities. Of the 72 species, 18 were considered prevalents in the sandsage type and 19 were considered prevalents in the adjacent areas (table 4). A total of 40 species occurred in both sandsage and adjacent community types; this accounts for the relatively large diversity values (table 3). Though the species diversity measurements were high, the differences between the two vegetation types were not significant.

Vegetation differences between sandsage and adjacent communities are shown in table 4. Shrub frequency was significantly higher in the adjacent communities. Perennial grasses and forbs occurred with significantly greater frequency ($p < 0.025$) within the sandsage community type. Cryptogams had higher frequencies in the adjacent communities as did annual grasses and total cover. Annual forbs showed no differences. Davis and Bonham (1979) reported related findings that sandsage canopy afforded protection to needle-and-threadgrass (Stipa comata) thus increasing its frequency on some sites.

Cluster analysis (fig. 2) was used to group study sites of similar vegetation type. Seven of the 10 sandsage communities clustered together with similarity indices ranging from 27 to 62 percent. Two of the three remaining

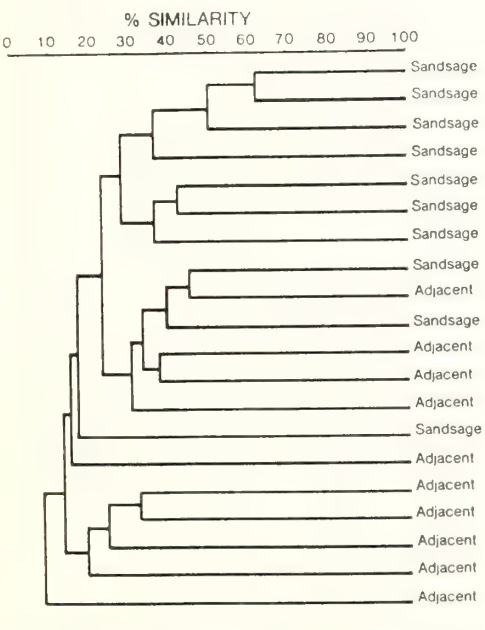

Figure 2.--Cluster dendogram of sandsage and adjacent communities.

sandsage communities were associated with a group of four adjacent sites. This association resulted from a large number of understory species occurring in both sandsage and adjacent communities.

The final sandsage community did not cluster with the other groups and had a similarity of 17 percent to the previously described clusters. The relatively low association level of this stand with the other sandsage sites was due to the increased frequency on this site of burweed (Ambrosia acanthicarpa) and threadleaf eriastrum (Eriastrum sparsiflorum). Extreme fluctuation in abundance of annual species from site to site is common in desert ecosystems and in our case, is considered responsible for the three sandsage sites not clustering with the sandsage group.

To explore species interactions, clusters on niche overlap were done for all species found in both types. Two groups in this cluster were of particular interest with respect to the sandsage community. Sandsage clustered tightly with four perennial understory species: Indian ricegrass (Oryzopsis hymenoides), sand dropseed (Sporobolus cryptandrus), sand verbena (Abronia villosa), and California croton (Croton californicus). These species are all highly adapted to sandy habitats. Though sandsage was strongly associated with this perennial herbaceous understory, its overlap with the most prevalent annual species in the community was only 9 percent. These annuals include red brome (Bromus rubens), cutleaf filarea (Erodium cicutarium), cheatgrass (Bromus tectorum), cryptantha (Cryptantha spp.), and six-weeks fescue (Vulpia octoflora). Two understory shrub species, little rabbitbrush (Chrysothamnus viscidiflorus) and snakeweed (Gutierrezia sarothrae) were tightly clustered with these annuals. Other groups were defined but were mainly associated with the adjacent community types.

To define these relationships more precisely, we employed the use of Cole's (1949) index of interspecific association (fig. 3; table 5). Two groups of species were apparent from the analysis. Both groups contain a mixture of perennial and annual species. Each group contains species which show positive affinities for species within that group and negative relationships (table 5) for the species found in the opposite group. The two groups are bridged by a single species of Cryptantha which had the highest percent frequency values of any species in the study. Such high frequency (48.3 percent) indicates that this species was very widespread across the study sites.

The analysis has shown the existence of two groups of understory species and indicates that these species are doing quite different things with respect to the sand pocket environments of sandsage in Washington County. The underlying reasons for the groupings are unknown, but they may be due to differences in microhabitat preferences or competitive relationships existent among the species themselves. Further study at this point is warranted.

Table 3.--Prevalent species occurring in sandsage and adjacent communities in Washington County, UT. Values represent average percent frequency

Species	Sandsage $\bar{X}$	Adjacent $\bar{X}$
Ambrosia acanthocarpa	6.0	0.2
Artemisia filifolia	42.4	Ø
Artemisia tridentata	Ø	4.9
Astragalus nuttalianus	Ø	8.8
Atriplex canescens	*T	5.4
Brickellia spp.	4.7	1.2
*Bromus rubens***	25.9	57.3
*Bromus tectorum***	47.0	32.9
Chrysothamnus viscidiflorus	2.5	12.6
Coleogyne ramosissimum	Ø	22.0
Croton californicus	3.9	Ø
*Cryptantha*** spp.	48.3	22.3
Eriogonum spp.	4.6	0.4
Eriogonum enflatum	Ø	7.4
*Eriophylum wallecii***	10.2	11.7
*Erodium cicutarium***	16.6	13.7
Gilia inconspicuum	1.0	10.6
Hilaria jamesii	3.8	5.8
Larrea tridentata	Ø	3.9
Lupinus alpestrus	6.8	Ø
Oenothera pallida	4.2	0.3
Oryzopsis hymenoides	14.2	2.1
Phacilia rotundifolia	Ø	5.8
Plantago insularis	1.8	5.2
Prunus fasiculatus	3.3	0.2
Psorothamnus fremontii	4.7	1.2
Schismis barbatus	1.4	8.9
Sporobolus cryptandrus	16.9	0.9
*Vulpia octoflora***	33.1	41.4
Gutierrezia sarothrae	4.7	16.7

*T = trace

** = Prevalent species in both sandsage and adjacent communities.

Table 4.--Means ($\bar{x}$) and standard deviations (SD) for vegetation factors and significance levels for the difference of the means observed in sandsage and adjacent communities in Washington County, UT. Significance levels were computed using the Student's t-statistic

Site factor	Sandsage		Adjacent	
	X	SD	X	SD
Total cover	24.2	6.93	31.8	11.42
Litter	89.7	8.81	86.7	27.90
Cryptograms	48.8	33.20	60.0	34.50
Shrubs***[1]	52.1	5.56	68.5	15.80
Perennial grass**	33.7	24.20	10.8	9.81
Annual grass	66.2	31.20	77.5	27.20
Perennial forbs*	19.2	22.50	3.9	4.34
Annual forbs	71.8	26.70	69.3	36.60
Diversity				
Shannon-Weaver's index	3.3	0.38	3.2	0.47
MacArthur's index	7.7	1.77	7.5	2.35

[1]Significance levels: * = 0.025; ** = 0.01; *** = 0.005.

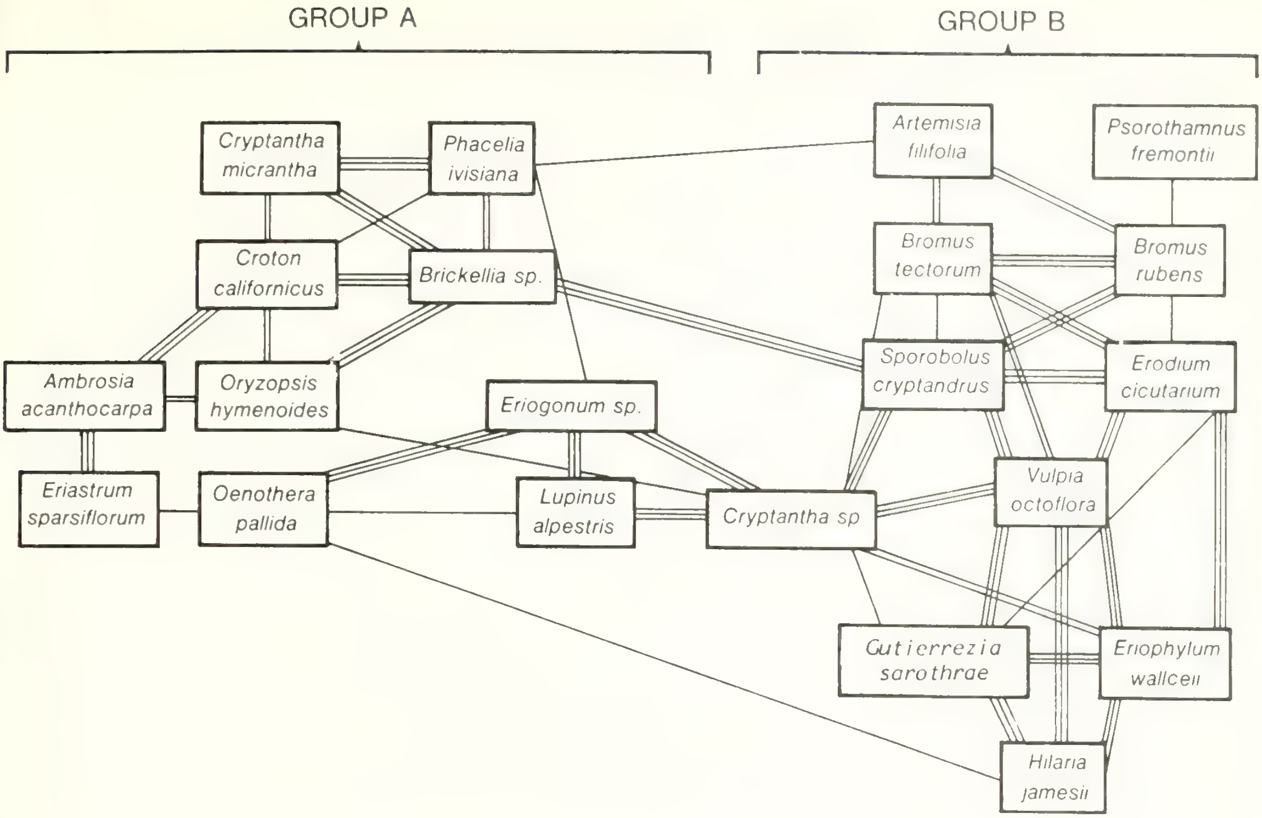

Figure 3.--Cluster diagram of positive interspecific associations between plant species occurring in the sandsage communities on Washington County, UT. Cluster is based on Cole's index of interspecific association and relates to species geographical distribution. The more lines between species, the more significant the association.

Table 5.--Results of Cole's index analyses with respect to the interspecific association patterns of species growing in the sandsage communities of Washington County, UT. Significance levels of the chi-square values are as follows: 0.05 = p ≤ 3.85; 0.01 = p ≤ 6.64; and 0.001 = p ≤ 11.21

	Positive associations				Negative associations			
Species	Species	x^2	Coef.	SD	Species	x^2	Coef.	SD
				GROUP A				
Ambrosia acanthocarpa	Croton californicus	11.5	0.203	0.060	Bromus tectorum	36.3	0.752	0.125
	Eriastrum sparsiflorum	65.1	0.491	0.060	Cryptantha spp.	18.5	0.695	0.161
	Oenothera pallida	6.1	0.139	0.057	Erodium cicutarium	10.5	1.000	0.308
	Oryzopsis hymenoides	8.6	0.361	0.123	Sporobolus cryptandrus	8.3	0.704	0.244
					Vulpia octoflora	19.5	0.852	0.193
					Gutierrezia sarothrae	5.5	1.000	0.427
Brickellia sp.	Croton californicus	30.5	0.319	0.058	Bromus rubens	4.2	0.380	0.185
	Cryptantha micrantha	46.2	0.493	0.073	Bromus tectorum	10.7	0.394	0.121
	Oryzopsis hymenoides	14.1	0.446	0.119	Cryptantha spp.	7.4	0.425	0.156
	Phacelia iviciana	9.6	0.147	0.047	Erodium cicutarium	4.2	0.610	0.297
	Sporobolus cryptandrus	16.2	0.460	0.114	Eriastrum sparsiflorum	4.7	1.000	0.459
					Eriophyllum wallecii	6.0	1.000	0.407
					Vulpia octoflora	4.0	0.375	0.187
					Gutierrezia sarothrae	5.9	1.000	0.412
Croton californicus	Cryptantha micrantha	10.9	0.239	0.073	Cryptantha spp.	7.4	0.425	0.156
	Oryzopsis hymenoides	6.7	0.308	0.119	Erodium cicutarium	6.2	0.740	0.298
	Phacelia iviciana	5.8	0.114	0.047	Eriophyllum wallecii	6.0	1.000	0.407
					Vulpia octoflora	9.8	0.583	0.186
Cryptahntha micrantha	Phacelia iviciana	13.4	0.138	0.038	Cryptantha spp.	65.2	1.000	0.124
					Eriastrum sparsiflorum	7.5	1.000	0.365
					Eriogonum spp.	4.4	1.000	0.476
					Eriophyllum wallecii	9.5	1.000	0.324
					Hileria jamesii	4.6	1.000	0.465
					Lupinus alpestris	7.5	1.000	0.365
Eriastrum sparsiflorum	Oenothera pallida	4.8	0.118	0.054				
Eriogonum spp.	Lupinus alpestris	176.7	1.000	0.075	Oryzopsis hymenoides	6.6	0.723	0.291
	Oenothera pallida	8.7	0.206	0.070	Sporobolus cryptandrus	7.8	0.854	0.302
	Phacelia iviciana	4.1	0.123	0.060				
Lupinus alpestris	Oenothers pallida	4.8	0.118	0.054	Oryzopsis hymenoides	8.7	0.657	0.223
					Sporobolus cryptandrus	12.5	0.819	0.232
					Gutierrezia sarothrae	6.1	1.000	0.406
Oenothera pallida					Sporobolus cryptandrus	10.2	0.796	0.249
Oryzopsis hymenoides					Vulpia octoflora	7.2	0.244	0.091
Phacelia iviciana					Vulpia octoflora	7.0	0.602	0.228
				GROUP B				
Artemisia filifolia	Bromus rubens	7.7	0.102	0.037				
	Bromus tectorum	10.9	0.187	0.057				
	Phacelia iviciana	5.0	0.027	0.012				
Bromus rubens	Bromus tectorum	11.9	0.307	0.089	Cryptantha micrantha	18.2	0.629	0.147
	Erodium cicutarium	6.4	0.091	0.036	Oenothera pallida	5.8	0.470	0.195
	Psorothamnus fremontii	5.6	0.043	0.018	Phacelia iviciana	7.2	0.605	0.226
	Sporobolus cryptandrus	11.8	0.156	0.045				
Bromus tectorum	Cryptantha spp.	6.2	0.112	0.045	Croton californicus	6.2	0.301	0.121
	Erodium cicutarium	25.1	0.117	0.023	Eriogonum spp.	7.2	0.413	0.154
	Sporobolus cryptandrus	5.8	0.071	0.029	Eriastrum sparsiflorum	14.9	0.457	0.119
	Vulpia octoflora	9.8	0.117	0.037	Lupinus alpestris	12.1	0.412	0.119
					Oenothera pallida	4.9	0.282	0.127
					Phacelia iviciana	7.3	0.398	0.147
Cryptantha spp.	Eriogonum spp.	9.9	0.047	0.015	Eriastrum sparsiflorum	8.6	0.340	0.153
	Erophyllum wallecii	10.8	0.073	0.022	Phacelia iviciana	7.1	0.505	0.189
	Lupinus alpestris	8.7	0.058	0.019	Psorothamnus fremontii	6.1	0.482	0.195
	Oryzopsis hymenoides	4.5	0.084	0.040				
	Sporobolus cryptandrus	7.9	0.107	0.038				
	Vulpia octoflora	12.2	0.169	0.048				
	Gutierrezia sarothrae	6.2	0.054	0.022				
Eriophyllum wallecii	Hileria jamesii	57.9	0.306	0.040	Lupinus alpestris	6.2	1.000	0.400
	Sporobolus cryptandrus	8.6	0.293	0.099	Oryzopsis hymenoides	5.1	0.455	0.197
	Vulpia octoflora	63.0	1.000	0.126	Phacelia iviciana	4.1	1.000	0.497
	Gutierrezia sarothrae	41.3	0.366	0.057	Psorothamnus fremontii	3.9	1.000	0.509
Erodium cicutarium	Eriophyllum wallecii	19.4	0.186	0.042	Eriogonum spp.	6.9	1.000	0.381
	Sporobolus cryptandrus	41.5	0.470	0.073	Lupinus alpestris	11.7	1.000	0.293
	Vulpia octoflora	49.0	0.645	0.092	Oenothera pallida	5.2	0.714	0.314
	Gutierrezia sarothrae	4.7	0.091	0.042	Psorothamnus fremontii	7.2	1.000	0.372
Hileria jamesii	Oenothera pallida	12.6	0.242	0.068	Sporobolus cryptandrus	6.0	0.722	0.295
	Vulpia octoflora	30.6	1.000	0.181				
	Gutierrezia sarothrae	20.3	0.368	0.082				
Psorothamnus fremontii					Vulpia octoflora	4.2	0.480	0.233
Sporobolus cryptandrus	Vulpia octoflora	12.4	0.257	0.073				
Vulpia octoflora	Gutierrezia sarothrae	26.2	0.133	0.026				

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ARTEMISIA REPRODUCTIVE STRATEGIES: A REVIEW

WITH EMPHASIS ON PLAINS SILVER SAGEBRUSH

Todd P. Walton, Richard S. White, and Carl L. Wambolt

ABSTRACT: Plains silver sagebrush (Artemisia cana Pursh ssp. cana) is a little-studied but important ecological dominant over much of the Missouri Plateau and peripheral zones east of the Continental Divide. Understanding the taxon's ecology and reproductive characteristics can be furthered by understanding related species. Knowledge of other Artemisia species and bits of specific silver sagebrush information provide a basis for research hypotheses needed for additional research of this species.

INTRODUCTION

The geographic range and ecological relationships of silver sagebrush (Artemisia cana Pursh) merit intensive research attention. However, this has not occurred. While big sagebrush (Artemisia tridentata Nutt.) has been studied extensively in recent years, biological information dealing with silver sagebrush is very limited. The western states rely heavily on range and pasture forage for their livestock industry. Therefore, appreciation of silver sagebrush communities and their implications for management is important.

Several adaptive features operate within the North American endemic Subgenus Tridentatae of the Genus Artemisia L. that have resulted in its extensive distribution and persistence in a variety of habitats. Features such as the ability to carry on photosynthesis at low temperatures, the ability to germinate over a wide range of temperatures, an extensive root system, and prominent secondary metabolic compounds may confer a competitive advantage for sagebrush (DePuit and Caldwell 1973; Caldwell 1978).

Two genetically different groups in the subgenus Tridentatae can be recognized. One group resprouts after disturbance (A. tripartita Rydb., A. cana Pursh, and A. rigida [Nutt.] Gray), while the other group does not (A. tridentata Nutt., A. arbuscula Nutt., A. longiloba [Osterh.] Beetle, A. nova A. Nels., A. bigelovii Gray, and A. pygmaea Gray).

Evidence indicates that all species and subspecies of Tridentatae can be given the status of topographic and edaphic climax dominants. As such, each defines a different niche. Many of the factors which influence the distribution patterns of sagebrush function through soil development combined with climatic or environmental characteristics (Hazlett and Hoffman 1975; Winward 1980; Froeming 1981). Several species such as silver and big sagebrush have achieved sufficiently wide distribution and have differentiation so as to have developed subspecific taxa. Big sagebrush is more widespread and has received the most research attention. Silver sagebrush is second in distribution but is not nearly so well researched.

SILVER SAGEBRUSH TAXONOMY

The silver sagebrush complex is composed of three subspecies with allopatric distribution (fig. 1) and characteristic ecological niches (Beetle 1977). Subspecies are separated morphologically on the basis of leaf width, sesquiterpene lactone content, and geography (Morris and others 1976).

Mountain silver sagebrush (A. cana Pursh ssp. viscidula [Osterh.]) is typified by greenish, linear leaves. It occurs on streambanks, meadows, and depressions generally at higher elevations. It is often found in close association with conifers in the Rocky Mountain region. Bolander silver sagebrush (A. cana Pursh ssp. bolanderi [Gray] Ward) has linear, canescent leaves and grows on poorly drained soils in central Oregon and eastern California. Plains silver sagebrush (A. cana Pursh ssp. cana) is an erect, canescent, freely branching shrub up to 5 feet (1.5 m) in height with large linear leaves. This taxon is found growing on well-watered, deep soils throughout the Northern Great Plains, especially along streambottoms and drainageways, in sparse to dense stands. Wyoming big sagebrush (A. tridentata Nutt. ssp. wyomingensis Beetle & Young) is the only other major shrubby sagebrush in the Northern Great Plains (Beetle 1977; Johnson 1978; Tisdale and Hironaka 1981).

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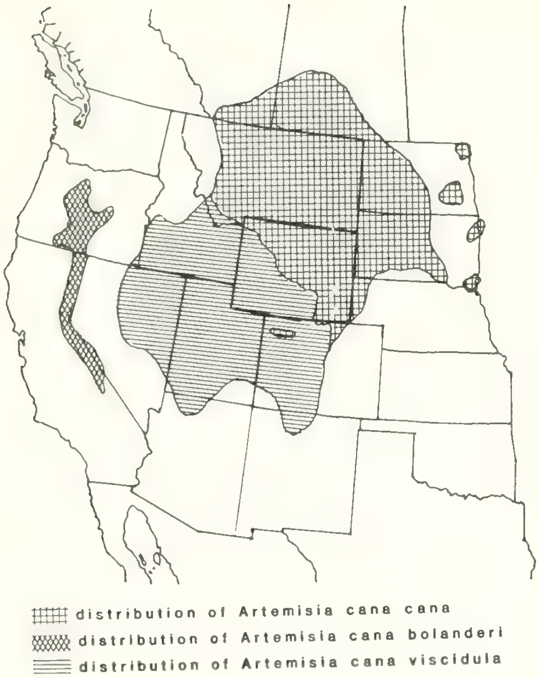

Figure 1.--Distribution of three subspecies of silver sagebrush in western North America (Harvey 1981).

DISTRIBUTION OF PLAINS SILVER SAGEBRUSH

Silver sagebrush occupies an estimated 34 million acres (14 million ha) in the 11 western United States (Beetle 1960). In Montana there are about 19.3 million acres (7.8 million ha) of big sagebrush and 12.8 million acres (5.2 million ha) of silver sagebrush, while in Wyoming there are 23.0 and 7.0 million acres (9.3 and 2.9 million ha) respectively.

Plains silver sagebrush occurs east of the Continental Divide (except for the Yampa River Valley, CO) in Wyoming and Montana north to southern Alberta and Saskatchewan and east to central North and South Dakota and northwest Nebraska. Several disjunct populations occur in the eastern Dakotas (Harvey 1981).

Plains silver sagebrush was first collected by Lewis and Clark on the bluffs of the Missouri River (Nuttall 1841). Typical habitats include loamy to sandy, well-drained upland soils and alluvial flats and terraces of valley bottoms. It is further distinguished as growing in dense or open stands along streams and valleys that are subject to erosion, flooding, and deposition. Hence, stratification and heterogeneity are conspicuous in the alluvial profiles (Thatcher 1959; Hazlett and Hoffman 1975; Johnson 1978). Thatcher (1959) noted that of the four sagebrush species he studied, only plains silver sagebrush grew on soils influenced by high water tables. Johnson (1978) reported that silver sagebrush and western wheatgrass (Agropyron smithii Rydb.) thrived together in areas of frequent flooding.

SOIL RELATIONSHIPS

Soil characteristics have been examined to evaluate their relationship to sagebrush distribution. Silver sagebrush prefers well-drained, alluvial, coarse-textured soils in bottomlands. Detailed soil and vegetation relationships in silver sagebrush communities have been reported. Lower levels of P, K, N, organic matter and cation exchange capacity were reported in soils where silver sagebrush dominated than in adjacent soils where big sagebrush was most abundant (Hazlett and Hoffman 1975). This was probably due to more mature soil development in the big sagebrush community. Cunningham (1971) reported that moderate to high levels of extractable magnesium in the 12- to 24-inch (31 to 61 cm) layer were important to the presence and success of silver sagebrush. This was associated with imperfect soil drainage and a shallow root system. Optimum habitat seemed to include a moist upper 6 inches (15 cm) of soil along with coarse materials in the soil profile.

Although similar research has not been done with silver sagebrush, Sturges (1977) states that water-use zones shift outward and downward in the soil from big sagebrush plants as the growing season advances. Sturges (1977) and Caldwell (1978) both characterize big sagebrush as having prominent, deep taproot with sufficient lateral spread and root density to capture summer precipitation. Deeper roots allow utilization of deeper water reserves.

FACTORS AFFECTING REPRODUCTION BY SEED

Allelopathy

Allelopathy has been extensively reviewed in the literature on Artemisia. This work has shown that allelopathy is prominent in Artemisia species throughout the world, and much foreign research focuses on it.

Allelopathic substances from Artemisia roots and leaves are universally thought to decrease respiration or inhibit germination of grass seed (Chirca and Fabian 1973; Friedman and others 197 Hoffman and Hazlett 1977; Weaver and Klarich 197 Groves and Anderson 1981; Hussain and Khanum 1982). In India, Melkania and others (1982) attributed the allelopathic potential of Artemis vulgaria L. to certain hydrophilic metabolites. In Japan, Numata and others (1975) found a biologically active agent (caffeic acid) in the roo of mugwort (Artemisia princeps Pampan.). Inhibition of grass germination has been the most commonly reported response, but in some cases stimulation of growth has been recorded (Hoffma and Hazlett 1977; Weaver and Klarich 1977; Chir and Fabian 1973). Hale (1982) noted that leachates from A. vulgaris L. also increased growth of the fungus Pythium myriotylum. Harve

(1981) observed autopathy in some sagebrush species in Montana, including plains silver sagebrush.

Seed Dispersal

One of the primary features of any reproductive strategy is the number of propagules that are produced and dispersed. In this respect, efficiency of seed dispersal by wind and reproductive capacity are associated. Sagebrush species are generally low in dispersal efficiency but high in seed production capacity (Bostock and Benton 1979). Seed dispersal is one of the most important factors promoting gene flow in plant populations. Dispersal is one way that plants can keep their descendants separated in space, and it provides each new plant with its own site where it has greater potential to compete with other plants (van der Pijl 1982). Dispersal strategy is complex and represents a compromise among conflicting demands. Consequently, in some species establishment might be more important than dispersal for achieving reproductive success. In most plant species, including sagebrush, dispersal seems to be incidental, especially during storms, and is not based on any special morphological structure.

Dispersal can play a critical role in determining population size. Because seeds of most plants are dispersed close to the parent, seed density falls off steeply as distance from the parent increases (Harper 1977; Cook 1980). This is the case with sagebrush (Beetle 1960; Friedman and Orshan 1975; Harvey 1981; Tisdale and Hironaka 1981; Walton 1984).

Seed dispersal in arid communities is described as falling into two classes (Mott 1979): (1) widespread dispersal, often of large numbers of seeds, enabling exploitation of a number of potential sites, and (2) utilization of a favorable habitat facilitated by minimal movement of seed from the parent plant. Under desert conditions, this second strategy is thought to improve the chances of seedling establishment since adjacent sites have already proved suitable for growth and development of parent plants (Friedman and Orshan 1975). Although dispersal is important, only a few dispersal patterns are noted by Cook (1980) as being published. In one such study, the patterns of achene dispersal, seedling emergence, appearance of cotyledons, and seedling mortality of _A. herba-alba_ Asso were related to distance from the parent plant. Eighty-five percent of the achenes of this species fell under the existing shrub canopy.

Sagebrush seed dispersal can be by animals, water, or wind (Tisdale and Hironaka 1981). However, the relative importance of each agent can vary. Although rodents play an active role in seed dispersal of many herbaceous species, no sagebrush seed was reportedly dispersed by rodents in Nevada (LaTourette and others 1971). However, Harvey (1981) believes that long-distance dispersal by silver sagebrush is probably due to mucilaginous seeds attaching to animals. Beetle (1960) declares that water is undoubtedly an important dispersal agent, but anemochory (wind dispersal) is more representative of Asteraceae (Compositae) and seems to be of greatest importance (Harper 1977; Bostock and Benton 1979; Evans and Young 1982). Seedlings of basin big sagebrush have been found up to 33 meters from the nearest possible source plant. Since sagebrush seeds have limited morphological mechanisms for distant wind-borne dispersal, the range of the plant is probably extended in contiguous bands around the periphery of established stands (Daubenmire 1975). Walton (1984) found that most seed was dispersed close to, or under, individual silver sagebrush plants. However, in at least one case, the largest proportion of seed was dispersed at 9.8 feet (3 m). In this instance, seed was evenly dispersed from the seed-bearing plant out to 9.8 feet (3 m), and there was no rapid decrease in dispersed seed until that distance was reached. Seed numbers then dropped off sharply.

Achenes of certain _Artemisia_ species, including silver sagebrush, develop a transparent gelatinous envelope around the seed upon contact with water (Clor and others 1974; Harvey 1981; van der Pijl 1982). This seems an important method for attaching to soil particles, thereby enhancing germination potential by protecting the delicate embryo from dessication and mechanical injury (Clor and others 1974; van der Pijl 1982). The mucilaginous seed coat has also been regarded as a dispersal agent, and in general, the drier the climate the more mucilaginous coating is present (Harvey 1981; van der Pijl 1982).

Phenological development in sagebrush results in most seed being shed during late fall and winter, although a few remain attached throughout the winter (Beetle 1960; Harvey 1981; Tisdale and Hironaka 1981). After the inflourescence reaches a seed-ripe condition, most viable seed is dispersed during the first 7 days. However, aborted florets and half-filled seeds are commonly dispersed over the following 2 to 4 weeks (Goodwin 1956). Tisdale and Hironaka (1981) have stated that up to 300,000 achenes per plant can be produced in big sagebrush, but Harvey (1981) reported a maximum production of only 54,000 achenes in silver sagebrush.

Germination Factors

Interest in germination characteristics of sagebrush is twofold. First, efforts to use sagebrush to provide forage or cover for livestock, wildlife, and erosion control depend upon this knowledge. Second, there is often a desire to reduce stand density in areas where plants become too abundant and compete with other forage plants (Pechanec and others 1965; McArthur and others 1974; Harvey 1981).

The combination of habitat conditions that favor seedling establishment has been referred to as a safe site (Harper 1977; Cook 1980). In this environment, the water, nutrient resources, and stimuli immediately surrounding a seed determine whether it will germinate (Harper 1977). Germination in a specific seedbed is also controlled by inherent characteristics of seeds, or in some

cases, through modification of the physical environment by the seed itself (Evans and Young 1982). Heterogeneity in the microenvironment and the extreme subtlety of germination requirements can determine the number and variety of seedlings that are recruited into the plant population from the seedbank. High-density stress can adversely affect seedling success. Another important element, herbivory, tends to diversify range plant communities. Herbivory within the local microenvironment influences seedling establishment and subsequent growth of plants, and therefore initiates regeneration cycles on a small scale.

One aspect of sagebrush communities is that very few Artemisia seeds germinate and survive beyond the first year (Evenari and others 1971; Hazlett and Hoffman 1975; Cook 1980; Harvey 1981), despite high annual seed production. Several factors contribute to this phenomenon including: soil matric potential with its effect on wetted contact between seed and soil (Collis-George and Hector 1966), early death of seedlings (Eddleman 1979), seasonal climatic conditions and plant age (Nosova 1973; Evans and Young 1982), and soil moisture relationships and litter (Beetle 1960).

Achenes of sagebrush in general do not exhibit specific germination requirements. Therefore, they are usually considered nondormant (McDonough and Harniss 1975; Caldwell 1978) and do not persist for long periods in the soil (Young and Evans 1975). However, if seeds are subjected to ideal laboratory conditions, germination can be as high as 90 percent (Harvey 1981). Important factors to examine, with respect to germination requirements, include cold treatments (stratification), temperature, light, water stress, and maturity of the seed.

Stratification.--Stratification has been defined as a cold treatment which breaks seed dormancy. It is important in many species. Bewley and Black (1982) state that it is most beneficial if seeds are hydrated. The amount of prechilling needed to enhance germination is quite variable among species and can range from a few days to several months (Young and Evans 1979; Bewley and Black 1982). It can also be unnecessary. Stidham and others (1980) state that most shrubs require prechilling to achieve maximum germination, and they identified big sagebrush in this category without regard to subspecies. Krueger and Shaner (1982) reported that prostrate spurge (Euphorbia supina Raf.) increased germination by 70-80 percent with stratification, but Krasikova (1978) showed that seeds of annual composites (Artemisia vulgaris L. included) were not affected by stratification. Because seeds of sagebrush species have been classified as nondormant, it might be hypothesized that such seeds would not benefit from prechilling. The only exception to this speculation has been mountain big sagebrush (McDonough and Harniss 1974; McDonough and Harniss 1975; Caldwell 1978). Stratification can also affect germination responses to environmental variables. In arrowleaf balsamroot (Balsamorhiza sagittata [Pursh] Nutt.), stratification lowered the optimum temperature for germination (Young and Evans 1979). In a similar fashion, prechilling significantly lessened the effect of water stress on germination of mountain big sagebrush seeds (McDonough and Harniss 1975). In plains silver sagebrush, stratification had no effect on germination success, probably due to seed not being dormant and therefore not requiring the dormancy-breaking cold treatment (Walton 1984).

Temperature.--The effects of temperature on seed germination have been studied extensively in many species. Temperature regimes are frequently involved in seasonal control of dormancy especially in response to interactions with light. An optimum temperature becomes apparent when seeds are germinated over a wide range. In addition, most seeds germinate better under constant rather than fluctuating temperature regimes (Bewley and Black 1982; Evans and Young 1982). Bewley and Black (1982) also note that rate of germination is of great value in characterizing seed responses to temperature, although there is often considerable variability due to genetic differences. This genetic heterogeneity is demonstrated through subpopulations of seed from a plant population. These subpopulations germinate under different temperature regimes and germination rates change with these temperatures. All subspecies of big sagebrush are noted to speed up germination from 2 to 18 days with increasing temperatures (McDonough and Harniss 1975). Sagebrush and other Artemisia seeds germinate over a wide range of temperatures, but optimum temperatures are usually well-defined (Weldon and others 1959; Clor and others 1974; Caldwell 1978; Krasikova 1978; Sabo and others 1979; Wilson 1982). In silver sagebrush, Harvey (1981) stated that the optimum seems to be about 57 °F (14 °C). However, Walton (1984) reported that higher temperatures of 68 °F (20 °C) were generally more favorable for germination when other factors such as osmotic potential and light regime were examined concomitantly.

Light.--Light can influence seed germination of Artemisia, depending on the species and associated environmental factors. Fringed sagewort (Artemisia frigida Willc.) germination required light, but this could be circumvented by treating seed with gibberillic acid (Wilson 1982). Sabo and others (1979) asserted that light had no effect on germination of either fringed sagewort or big sagebrush seed. However, evidence to the contrary has been presented that states that light increased germination by as much as three times in big sagebrush (Weldon and others 1959). The germination response that has been observed in other species clearly demonstrates that light could play a role in the germination of silver sagebrush. This has been confirmed by Walton (1984).

Osmotic potential.--The specific effects of osmotic potential on silver sagebrush are little known. However, big sagebrush responded to more negative osmotic potential with less total germination, but this was ameliorated by light (Weldon and others 1959). In contrast, Sabo and others (1979) reported little effect of osmotic potential until 10 atm (1.0 MPa) was reached. Fringed sagewort was much more sensitive than big sagebrush and showed initial responses at 2 atm

0.2 MPa). Walton (1984) found germination ercentages and rates dropped off steeply under he influence of more negative osmotic potentials, nd no germination was observed below -7.5 bars -0.75 MPa).

aturity of seed.--Maturity of seed does have an ffect on plains silver sagebrush germination with igher values being observed in later seed collecions (Walton 1984). Clor and others (1974) eported that Artemisia herba-alba reacted this ay, and both prostrate spurge and prostrate ochia (Kochia prostrata [L.] Schrad.) showed igher germination percentages when seed was ollected later (Waller and others 1980; Krueger nd Shaner 1982).

LANT ESTABLISHMENT

fter seeds have germinated, reproductive success epends ultimately upon successful emergence from he soil, survival as a young seedling, and growth o maturity as a seed producer. Although Hickman 1979) pointed out that at least 95 percent of all lant mortality occurs within the first year, eedling demography has not received extensive esearch attention. In addition, a priori logic s sometimes used to conclude that most, if not ll, seedlings will reach reproductive maturity if ney can survive the first growing season. In rtemisia species, little is known about seedling ynamics.

lthough sagebrush seed production is high, very ew seedlings emerge and survive. Walton (1984) ound that only 1.2 percent of field-planted ilver sagebrush seeds emerged, but only 11 ercent of these seedlings survived the first rowing season. This can be attributed to the nount of competitive vegetation, litter, adverse nvironmental factors such as water stress and epth of burial, and allelopathy (autopathy) Johnson and Payne 1968; Evenari and others 1971; riedman and Orshan 1975; Eddleman 1979; Cook 980; Harvey 1981; Evans and Young 1982; Wilson 982). Depth of seed burial also influences emerence. The maximum depth from which sagebrush eed will emerge has been estimated at 0.2 inches mm) by Harvey (1981). Burial at 0.08 inches mm) was considered an optimum depth for plains ilver sagebrush. However, Walton (1984) reported hat more seeds planted at 0.2 inches (5 mm) roduced seedlings in the field than at depths of and 0.6 inches (0 and 15 mm). In addition, ortality was least for those emerging from 0.6 5 mm). Years that are favorable for seedling stablishment can occur at irregular intervals. he primary controlling factor is soil moisture Johnson and Payne 1968; Gordon and Wright 1981).

rowth characteristics of sagebrush seedlings seem be primarily subject to genetic control though environmental influences also contribute seedling response. Among big sagebrush accesons and subspecies, growth parameters showed gnificant differences in each measure. Height, rown, length of leaders, and annual yield were mong the parameters differing between accessions nd subspecies (McArthur and Welch 1982).

VEGETATIVE (ASEXUAL) REPRODUCTION

Vegetative reproduction in Artemisia has been examined, but few in-depth studies have been completed. Bostock and Benton (1979) studied five perennial composites with varying degrees of lateral extension and growth. They subsequently related seed and vegetative reproduction strategies. Seed was generally more important than vegetative capacity. However, Artemisia vulgaris L. perennates only by vegetatively produced propagules, and it has rhizome growth measured at 11.8 inches (30 cm) per year.

Went (1979) contends that survival of perennial desert plants depends mainly upon vegetative reproduction, and seeds are only a secondary method of reproduction that becomes important when summer rains allow abundant germination. Contradictory evidence has been presented in a study by Young and Evans (1972). They examined green rabbitbrush which was long thought to invade sites by root sprouting. They discovered that it relied heavily on seed dispersal to establish new plants. Apparently either mechanism can be successful.

There are special problems that vegetative reproduction presents for the field and experimental ecologist. Abrahamson (1980) stated that vegetative reproduction is more similar to growth than to reproduction with confusion coming from using animals as models. He stated further that vegetative reproduction is a distinct and well-defined phenomenon.

Clonal reproduction is common in forest herbs, aquatic plants, and at higher altitudes and latitudes where ecosystems are often influenced by fire, climatic, and other disturbances (Abrahamson 1980; Legere and Payette 1981). A clone can be defined as the aggregate of individual organisms descended by asexual reproduction from a single sexually-produced individual (Barnes 1966). Plants in such diverse genera as Ophioglossum, Pteridium, Populus, Equisetum, Carex, Rhus, Cornus, Prunus, and Artemisia form clones by initiating shoots from underground parts. Clonal growth is much more prevalent in many species than sexual reproduction, in spite of the fact that there may be a large and viable seedbank in the soil (Evenari and others 1971; Hazlett and Hoffman 1975; Cook 1980; Harvey 1981; Lovett-Doust 1981). Silver sagebrush stem cuttings may root within 8 weeks when collected at the leaf growth phenological stage (Everett and others 1978). Walton (1984) discovered that, in nearly every instance, plains silver sagebrush showed some degree of rhizomatous growth, even among small seedlings.

Soil texture influences what reproductive strategy is favored. Higher clay content usually favors vegetative reproduction. Increasing litter decreased the success of vegetative reproduction, while increased environmental severity accentuated it (Abrahamson 1980).

CONCLUSION

As shown in this review, specific information on the reproductive strategies of plains silver sagebrush is lacking. However, the bits of specific information available coupled with knowledge of other members of the genus Artemisia provide a basis for formulating research hypotheses to further investigate this important, but relatively ignored, taxon.

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ECOLOGICAL ADAPTATION AND GRAZING RESPONSE OF BUDSAGE (ARTEMISIA SPINESCENS)

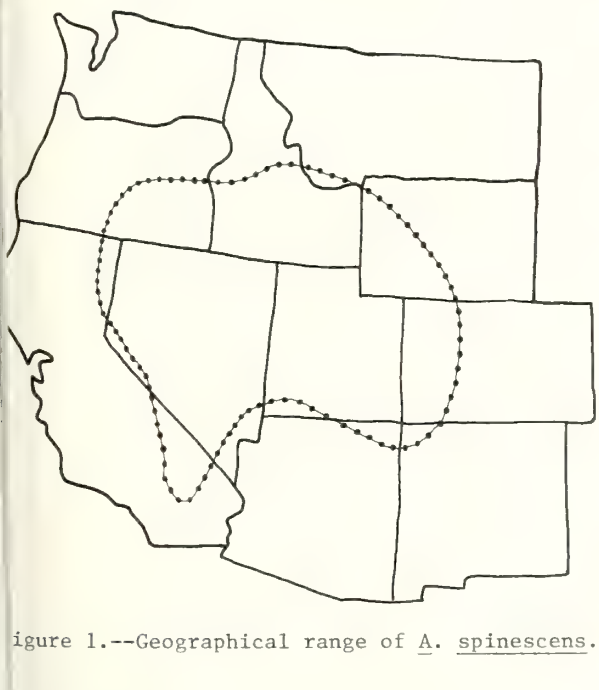
IN SOUTHWESTERN UTAH

Benjamin W. Wood and Jack D. Brotherson

\BSTRACT: Several Artemisia spinescens sites representing different plant communities and different grazing histories were studied to investigate physical adaptations and the influence of grazing on this species. Summer dormancy and root growth patterns indicate methods of adaptation. Grazing records show that late winter grazing could be very detrimental to A. spinescens growth and survival.

:NTRODUCTION

Budsage (Artemisia spinescens D. C. Eaton) is one of the more common perennial shrubs growing on the semiarid valley bottoms and benches of the Great Basin of the western United States (fig. 1). This species was first described as Picrothanmus desertorum by Nuttall (1841). In 1871, D. C. Eaton placed this plant in Artemisia because the flowers are reduced and have a tendency toward fusion of the style-branches of the disk flowers. Budsage is well set off as a species by its spinescent habit and consistent characteristics in the involucre and floral parts. The harsh environment where it grows has undoubtedly helped to stabilize the species so that variants do not occur or are at least unknown. Budsage is not known to hybridize with any other species.



igure 1.--Geographical range of A. spinescens.

Unlike most of the woody species of the genus, budsage is deciduous. The leaves normally fall off the plant by midsummer. Budsage is easily recognized in all seasons of the year. It is one of the first shrubs to become green in early spring (fig. 2A) and has a gray-green foliate. During the summer and winter (fig. 2B), it can

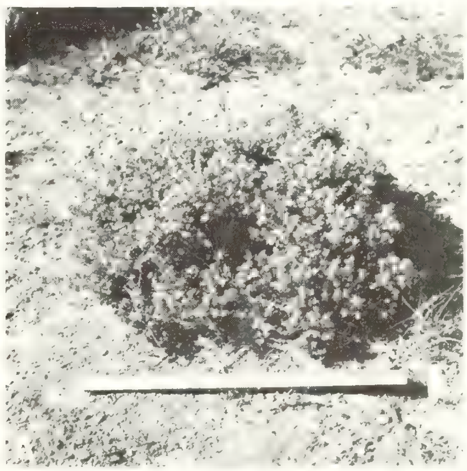
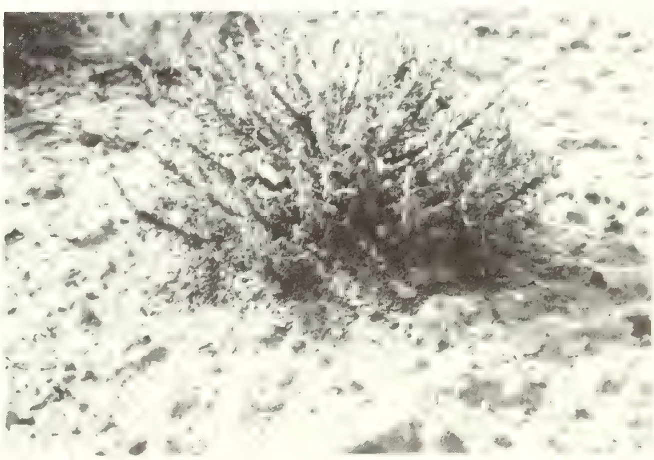


Figure 2.--Habit of A. spinescens during the spring (A), summer and winter (B) seasons. Rule in "2A" is 20 inches (50.8 cm) long. Plant in "B" is 15 inches (38.1 cm) in diameter.



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be recognized by its spiny habit and absence of leaves. This shrub is also pungently aromatic.

When the plant first shows signs of breaking dormancy, but before the buds elongate, the bark can be easily removed from last season's growth by pulling action. It is at this time that budsage becomes palatable to sheep. This condition is referred to by sheepmen as "slipping". Budsage is one of the most palatable forage species on sheep winter range during the late winter and early spring (Hutchings 1954: Dayton 1931). This relatively short period of time (generally February and March) closely coincides with the period of slipping. Such early availability is important on sheep range because budsage adds high quality nutrition to sheep diets at or about the time of lambing (table 1). Although most winter forage plants are borderline to decidedly deficient in digestible protein, phosphorus, and metabolizable energy (Cook and others 1954), budsage has especially high calcium, magnesium, and phosphorus content (Millar 1958). Its protein content is also high.

After the new twigs have elongated somewhat, it palatability drops because the content of volatile oils increases (Cook and others 1954) and because other plants such as grasses and winterfat (Ceratoides lanata) become green. Cattle and horses seldom utilize budsage, possibly because of its aromatic oil content.

Wild game such as mule deer (Odocoileus heminonus) and pronghorn antelope (Antilocapra americana) utilize this species during the spring while it is green and succulent. Mountain sheep (Ovis canadensis) eat it in the summer when it is dry (Gullion 1964).

Black-tailed jackrabbits (Lepus californicus) and small rodents generally eat only the leave smaller branches and twigs. However, black-tailed jackrabbits may occasionally prun back a whole plant. Harper and others (1958) reported that Chucker partridge (Alectoris graeca) eat the flower heads and leaves.

Hall and Clements (1923) reported there is som evidence that calves have been poisoned by eating the green foliage. They also noted tha the pollen of budsage is a cause of hay fever.

Table 1.--Summary of forage values of Artemisia spinescens under average range conditions[1] of the Great Basin (Cook and Harris 1950; Cook and others 1954; Cook and Harris 1968)

			Protein						Energy			
	Cellulose	TN	Digestible	Consumed	Total	Carotene	Ca	P	Gross	Metabolizable	Eaten	Digestible
	(%)	(%)	(%)	(%)	(%)	(mg/lb)	(%)	(%)	(cal/lb)		(cal)	(cal)
Optimum intake:												
Artemisia spinescens 3.30 lbs/day - oven-dried (under range conditions for a 130-lb ewe)			2.60	0.09	4.3-5.4			0.09	1587-1693	577	1904	
Average intake:			4.70			7.20		0.12		614		
Browse species 3.5-3.6 lbs/day - oven-dried (under range conditions for a 130-lb ewe)												
A. spinescens:												
Green, spring growth	18.1	50.6			9.79	10.20	0.97	0.09	1923			1160
In saltbush communities			13.70				1.32	0.33		911		
In sagebrush communities			13.70					0.33		911		
Heavily grazed (70% utilization) 4.20 lbs/day - oven-dried			13.70		17.30	10.80		0.33		911		
Digestion coefficient	58.1				79.10				60.3			

[1]Average range conditions:

	Production	Utilization	Floral composition of diet	Species composition
Artemisia spinescens	1 lb/acre	53%	7%	1 to 5%
Browse species	255 lb/acre	24%	83%	74%

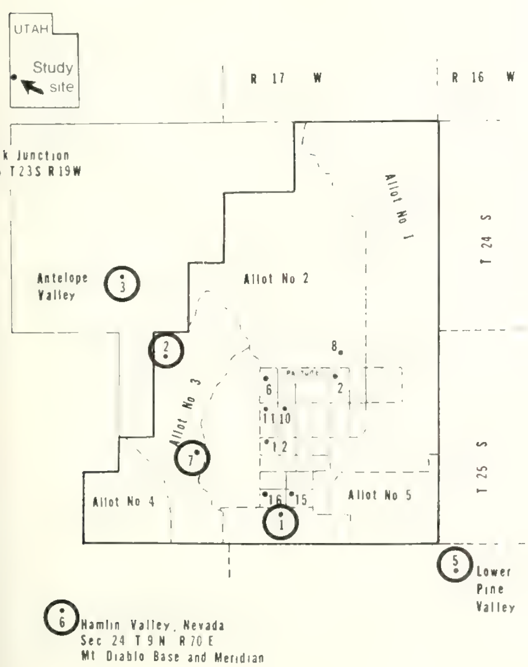
his study of budsage's ecological life history as undertaken to determine how it has adapted o the rather harsh environment of southwest tah and bordering Nevada and to investigate the nfluence of sheep grazing upon its survival and eproduction.

TUDY AREA AND METHOD

his study was conducted from 1963 to 1965 in estern Millard County, UT, and adjacent White ine County, NV (fig. 3). Specific study sites ere located at seven locations where budsage rows in Pine, Antelope, Snake, and Hamlin alleys. Most of the sites in Pine Valley were n the Desert Experimental Range (DER) which is aintained by the U.S. Department of griculture, Forest Service, Intermountain esearch Station. Those in the other valleys e on land managed by the U.S. Department of ie Interior Bureau of Land Management. The udy sites were selected as being representa- ive of the different communities in which idsage occurs. They also represent different razing histories and treatments of winter sheep inge (table 2).

limate

ie precipitation of the area is not evenly istributed throughout the year. During April, iy, July, August, and October, the area eceives about 57 percent of the total ecipitation; during July and August it eceives almost as much as the other three onths combined. The area receives the least nount of moisture in January and December.



gure 3.--Location of study sites. Circled mbers indicate study sites and correspond to te numbers used in text.

Drought is not uncommon to the desert; great fluctuations in annual and monthly precipitation are characteristic. During a 30-year period for which climatological data have been recorded at the Desert Experimental Range (DER), the area has, at least once, received no measurable precipitation during each month.

The summers are warm, and midday temperatures are usually above 90 °F (32 °C). The winter temperatures vary considerably and sometimes are very cold. The temperature extremes may be from -26 °F (-34 °C) in the winter to about 100 °F (38 °C) in the summer.

The weather during the study period was somewhat unusual because the summers of 1963 and 1965 were some of the wettest recorded at the DER. Summer precipitation was 5.10, 1.38, and 5.03 inches for 1963, 1964, and 1965, respectively. The precipitation in late summer of 1963 and 1965 was sufficient to moisten the root zone of natural seedlings during the last week in August and September, but that of 1964 did not moisten the root zone.

The winds are frequent and may be of rather high velocity. The monthly means are between 4 to 6 miles per hour (6.4 and 9.7 km per hour) with gales reaching 15 to 30 miles per hour (24.1 to 48.3 km per hour) (DER water station records). Scarcely a day passes without some wind. This reduces the intensity of the high summer temperatures, but also increases the rate of evaporation to which the plants and soil are subjected.

Soils

Soil pits were dug and sampled to ascertain the various soil conditions tolerated by budsage. Vest (1962) reported that near Dugway Valley, UT, budsage grows only on clay loams and sandy clay loams. He also indicated budsage showed the narrowest tolerances to changes in soil texture of all the species he studied. However, at the DER and adjacent areas, this species grows in soils ranging from sandy to loam textures, indicating it has a wider tolerance to soil texture than previously reported.

Each soil was sampled by horizons. Analyses were completed using duplicate samples representing the horizons. Averages of the data obtained are reported. The presence and relative amounts of carbonates in the soil were determined by the effervescence caused by 0.1 N hydrochloric acid (Wood 1966).

Soil textural analyses were made by the hydrometer method of Bouyoucos (1951) using sodium silicate as the dispersing agent. The exchangeable bases were determined by leaching 25-gram soil samples with 200 ml of 1 N ammonium acetate and then determining the amount of cations present using a flame spectrophotometer. The amount of each cation present is expressed in milliequivalents per 100 grams of soil.

Table 2.--Grazing history, elevation, exposure, and dominant vegetation of principal study sites. The Hamlin Valley site is according to the Mt. Diablo Base and Meridian; all other sites reckoned from Salt Lake Base and Meridian. Site numbers correspond to numbers used for sites in text

Site number		Elevation (meters)	Slope (%)	Exposure	Dominant vegetation
Ungrazed #1	Ungrazed area of west DER headquarters T25S R17W Sec. 33.	1615	1	NE	*A. spinescens*, *A. confertifolia*, *C. lanata*, *Oryzopsis hymenoides*, *Hilaria jamesii*
Grazed #2	Grazed by sheep at specific times in winter and early spring. Unit 3 or DER Allotment 3. T25S R18W Sec. 2.	1768	3	W	*Artemisia spinescens*, *Ceratoides lanata*
Grazed #3	Grazed by sheep all winter. Antelope Valley. T24S R18W Sec. 26.	1798	1.5	SW	*Atriplex confertifolia*, *Artemisia spinescens*
Grazed #4	Grazed by cattle in winter and early spring. Burbank Junction. T23S R19W Sec. 16.	1652	0	Flat	*Sarcobatus vermiculatus*, *Artemisia spinescens*, *Atriplex confertifolia*
Grazed #5	Grazed by cattle in winter and early spring. Lower Pine Valley T36S R16W Sec. 6.	1567	0	Flat	*Atriplex confertifolia*, *Artemisia spinescens*, *O. hymenoides*, *H. jamesii*
Grazed #6	Grazed by cattle in winter and early spring. Hamlin Valley. T9N R70E Sec. 24.	1737	2	NW	*Artemisia spinescens*, *Ceratoides lanata*
Grazed #7	Grazed by cattle in winter and early spring. Warm Cove. T25S R18W Sec. 24.	2438	3	S	*Atriplex confertifolia*, *Artemisia spinescens*

Soil salinity was determined by measuring resistance of a saturated soil paste with a Wheatstone electrical conductivity bridge. Data are expressed in parts per million of soluble salt in the soil. A Beckman glass electrode pH meter was used to determine the hydrogen ion concentration of saturated soil samples.

The parent material of the soils is alluvial in origin, derived principally from Paleozoic sedimentaries. The soil surface between the plants is nearly always covered with an erosion pavement of gravel or rock of uniform size. It is usually dark in contrast to the light gray soil beneath.

The soils that support budsage have markedly less gravel between 20 and 30 inches deep than those supporting other vegetation. This zone of less gravel is also a zone of lime accumulation. The soils of the adjacent shadscale-winterfat (*A. confertifolia* - *C. lanata*) type contain less gravel in the upper horizons than surrounding types. These soils were also less saline and deeper than those supporting adjacent winterfat and shadscale communities.

Soil moisture content was studied at four locations and at three depths: 0-5.1 cm, 15.24-20.32 cm, and 25.40-30.5 cm. These depth were chosen because budsage is a relatively shallow-rooted plant. Soil moisture indices were determined using pressure membranes. The moisture content held in the soils at 1/3 and 1 atmospheres of pressure is expressed as a percentage of the oven dry weight of the soil. The soil moisture content was determined using "speedy" Soil Moisture Tester apparatus that measures moisture by a calcium carbide gas method. The moisture content is expressed as a percentage of the dry weight. The moisture holding capacity of the soils is less than 10 percent in the first 2 feet. Soil moisture increased only after rains in the fall; the summer rains did not generally penetrate more than 5.7-7.6 cm deep, except in washes and outwash areas. In this arid area, essentially all the moisture from light to moderate summer showers may be lost by evaporation within 1 to hours after the storm is over. The desert soil are very dry during the rather long summer period. This is the period which budsage evade by becoming dormant.

Some plants modify the characteristics of the soil in which they grow, especially the rate of water infiltration. For example, moisture infiltrates faster and penetrates deeper into the soil under budsage plants than under Indian ricegrass (O. hymenoides), shadscale, or winterfat. This phenomenon was observed to occur more frequently in sandy soils than those having a silty texture.

Plant Communities

The various plant communities at the sites can be classed into three broad vegetation types, budsage-winterfat, shadscale including winterfat, and shadscale without winterfat.

The shadscale with winterfat type is a mixed shrub community that contains a substantial amount of grasses. Data reported here for this type were from an ungrazed area. Other data from an area grazed moderately by sheep in early or late winter in alternate years indicate the important grass species is sand dropseed (Sporobolus cryptandrus) as opposed to Indian ricegrass and galleta (Hilara jamesii).

The shadscale communities contained very few other perennial species except galleta. Annual species such as Russian thistle (Salsola iberica) and halogeton (Halogeton glomeratus) were abundant. The communities studied were grazed all winter long, and such grazing has probably eliminated any winterfat and perennial grasses that may have been present. These communities are in the valley bottoms rather far from the mountains.

Budsage is not restricted to these community types; it grows in almost every type of desert community that occurs on benches or low-lands of the Cold Desert or Northern Desert Shrub Formation (Shantz 1925) of the Great Basin and to some extent of the Colorado Plateau. It is particularly abundant on plains and high mesas of northern Nevada, usually growing on moderately alkaline soils (Shreve 1942). Budsage is commonly associated with species of the salt-desert or salt-bush formation as defined by Hutchings and Stewart (1953), Harrington (1954), Gates and others (1956), and Bronson (1966); not that defined by Shantz (1925) which was a greasewood formation, although budsage does occur with greasewood (Sarcobatus vermiculatus).

Plant Measurements

At each of five sites, 60 plants were chosen at random and the total number of current year's vegetative twigs and current year's spines on each plant were counted. The spine/vegetative twig ratio was computed from these data in 1964 and 1965. These data were obtained from two DER pastures and an allotment which are moderately grazed in winter, from a BLM range allotment which is heavily grazed all winter long, and from a protected area in one of the above pastures.

Cover estimates were made in 1964 on grazed and protected plots or sites located in four experimental pastures, two grazed at a heavy and two at a light rate of stocking with sheep. These pastures also represent grazing in mid and late winter. The 1964 data were compared with the cover data obtained in 1934 when the pastures were established.

Cover estimates were obtained using the line-intercept method (Canfield 1941) and the line-point method which is a modification of the point-frame method of Levy and Madden (1933). These methods give cover data from which the percentage of bare soil, litter, plant cover, plant composition, and foliage cover were calculated. At each location six 100 foot transects were used.

Percentage of plant composition was calculated by dividing the total sum of the intercepts of each species by the total of all vegetational intercepts at each location times 100.

The percentage cover composition data from four experimental pastures are reported in table 3. Two kinds of composition are reported: the relative amounts of shrubs, forbs, and grasses in the total plant cover, and the relative amounts of different species in the shrub component. Plant counts (density) of budsage and three associated species, (shadscale, winterfat, and Indian ricegrass) were made on the same plots where the cover data were obtained and on plots in two additional pastures. Plant counts were made using 1 m^2 plots at each location and from these data density was calculated. Density was determined by dividing the total number of plants of a species by the total area sampled.

Phenology

Plant growth and development of 32 budsage seedlings growing on an area of past intense disturbance by burrowing rodents were observed and recorded during the summers of 1963 and 1964. The plants were one year old in 1963. One-half of these plants were watered once a week for eight weeks beginning in mid-June of both years before the plants became summer dormant. Several other seedlings in the same area were dug up in September and November of 1963 and April, June, July, and August of 1964 to compare the root systems of watered and nonwatered plants.

Plant growth and development studies of mature budsage plants were made. Plant collections were made in August, September, and November of 1963. Plants were also collected about every two weeks beginning in late February through June of 1964. From these collections data on leaf, stem, flower stalk lengths, and age of flowering were obtained as well as the time of growth.

Table 3.--Percentage cover composition from 40 200-square-foot plots in each enclosure and adjacent grazed acre in four experimental pastures of DER. Light grazing = 49% utilization (10 sheep days per acre). Heavy grazing = 68% utilization (17 sheep days per acre)

	Light grazing								Heavy grazing							
	Midwinter - Pasture 11				Late-winter - Pasture 10				Midwinter - Pasture 12				Late-winter - Pasture 15			
	Enclosure		Grazed		Enclosure		Grazed		Enclosure		Grazed		Enclosure		Grazed	
	1935	1964	1935	1964	1935	1964	1935	1964	1935	1964	1935	1964	1935	1964	1935	1964
Grasses	53.5	43.2	53.8	37.8	52.9	16.9	59.7	46.7	45.0	18.1	25.3	31.7	5.6	5.9	10.9	17.6
Forbs	8.6	5.5	9.9	9.9	3.0	7.0	4.8	6.7	11.0	7.5	1.2	7.5	0.1	1.4	0.5	4.7
Shrubs	37.8	51.3	36.3	52.3	44.1	76.0	35.5	46.6	44.0	74.4	73.5	60.8	94.3	93.7	88.6	77.7
Atremisia spinescens	22.3	48.7	25.7	26.5	41.4	56.6	36.2	8.4	20.2	59.1	22.3	28.8	4.5	35.7	3.8	0.8
Atriplex confertifolia	77.5	48.7	74.1	73.0	56.8	43.2	52.9	88.0	79.7	40.8	74.4	66.2	42.4	10.7	42.3	0.8
Ceratoides lanata	0.1	0.6	--	--	--	--	0.2	0.5	0.1	0.1	3.3	5.0	53.1	53.1	53.9	55.7
Kochia vestita	--	--	--	--	--	--	--	--	--	--	--	--	--	0.3	--	--
Chrysothamnus viscidiflorus stenophyllus	--	--	--	--	--	--	--	--	--	--	--	--	--	0.2	--	--
Ephedra nevadensis	--	2.0	0.2	0.5	1.5	--	10.2	2.6	--	--	--	--	--	--	--	--
Polygala subspinosa	--	--	--	--	0.3	0.2	--	--	--	--	--	--	--	--	--	--
Gutierrezia sarothrae	--	--	--	--	--	--	0.5	0.5	--	--	--	--	--	--	--	--

Root growth was studied by digging small trenches 1 foot wide by 2 feet deep and 3 feet long along one side of a budsage plant. This was done in August, 1963. All of the roots of the plant were removed from the trench. The roots were also removed from the soil taken from the trench by screening it before it was replaced back into the trench.

The trench was dug again in November, 1963, February, 1964, and June, 1964. When the trenches were redug all of the new roots were obtained by screening the soil taken out of the trench. The amount of growth was determined by measuring the total length of new root segments collected. In addition, some other plants were also dug up with the greatest possible care, and the root systems were mapped to scale. Seedling budsage, 2- and 4-year-old budsage specimens, and specimens 4 inches high were excavated and drawn to scale to compare the development of the root system as the plant matured.

Ring counts were made on 25 plants in each of four size classes. The plants were cut at the ground level, because this is usually below the point where the plant is branched. The ring count inspection was confined to the pattern of growth layers between adjacent rays.

RESULTS AND DISCUSSION

Seedling Development

Budsage seedlings have two very small orbiculate dark green cotyledons. The seedlings grew rapidly and in 10 days from planting some seedlings grown in moist sandy soil had some deeply lobed leaves and were 10.2 mm high. The lowest leaves were lobed and the upper ones entire. The roots were 5-7 inches (12.7-17.8 cm) long having several short branchlets. If the soil was allowed to dry out during the first 20-30 days of development, the seedlings died. This was true whether the plants were planted in soil flats or growing naturally. During the first year of growth, the shoot did not grow more than 3/8-7/16 inches (8.5-11 mm) high and the roots grew to 5-8 inches (12.7-20.3 cm) deep.

In 1963 a group of natural seedlings was given supplemental water and a comparable group was not. The former group broke summer dormancy August 28, and the latter group broke summer dormancy 2 weeks later. The total growth displayed by either group was, however, essentially the same when cold weather began in late September; all plants produced one or two twigs bearing leaves up to 5.5 mm long. The following spring, no difference in growth could be detected between the two groups. Before the seedlings became summer dormant, they produced an average of four new lateral twigs and one terminal twig that were 6.3 to 19.0 mm long. These plants became dormant by June 21, 1964.

During the summer of 1964, the seedlings received the same treatments as in 1963. Those that did not receive supplemental water remained dormant throughout the summer. The group that received supplemental water began to break dormancy in mid-July. The only obvious growth was new leaves. However, not all of the young plants produced new leaves, although all produced new root growth. At the end of the summer, the group that was watered had root systems considerably larger than the one that was not watered.

Plant Growth and Development

Budsage broke dormancy by late August of 1963 in response to storms that yielded sufficient moisture to penetrate the soil 25.4 to 30.5 cm. The terminal buds burst and produced small, new leaves; the stems did not elongate. The stems remained very short, mostly within the protecting petiole base of the previous year's leaf in whose axil they were growing, until the following March when elongation occurred. The maximum leaf length produced that fall was 5 mm. From plants that were dug up, it was obvious that the greatest amount of growth in the early fall was in the root system. The tap roots had produced many new branch roots.

Shortly after the plants broke dormancy in late August, the stems began to slip. Sheep grazed budsage from the time they arrived on the winter range in November 1963 through April 1964. Previously, slipping and the grazing period of this species were thought to occur only in late winter or early spring (Cook and others 1954).

The precipitation of the summer of 1964 was not enough to permit breaking of dormancy in budsage as in 1963, and the plants did not slip or become usable browse for sheep until March 1965. But the late summer of 1965 again brought abundant moisture and slipping occurred early in the fall. Once again, as 2 years earlier, budsage was browsed by sheep throughout the following winter.

In the late summer and fall of 1963, storms over the northern portion of the DER yielded enough rain so that the soil was visibly moist from the surface down to 30.5 cm by the first of September. Near the valley bottoms, moisture was visible down to 38.1-45.7 cm deep at the end of November. The maximum depth was 50.8 cm to which the moisture penetrated during the fall and winter before budsage began to elongate in March 1964.

The wetting front of the soil from Site 4 was below 1.2 m throughout the entire summer in both 1963 and 1964. Budsage is sufficiently deeply rooted at this location that the onset of summer dormancy is usually 2 weeks later than that observed at the other study sites.

In most years and on most sites, the annual growth of budsage is completed by the first of June. The terminal and lateral buds generally expand and begin to elongate in late March and early April at the latter part of the slipping period. Bud burst has been recorded as early as February 6 and as late as April 13.

Leaves and flower heads usually begin to turn brown in early June; by the third week of June, both were falling off the plants. All the leaves and flowers were gone by the first week of July, and the annual growing cycle was completed. In years of spring drought, summer dormancy may occur in early June.

Flowering

In general, flower buds begin to elongate two weeks later than vegetative buds. However, in February 1964, some floral buds located just below the terminal buds on the previous season's growth elongated to 6 to 9 mm long.

Budsage usually blooms from the last week of April through the last week of May. It has been found from herbarium specimens that this species has bloomed as early as March 29 at 6000 feet (1829 m) elevation in White Pine County, NV. (Moore m 537, Brigham Young University Herbarium) and March 24 at 2700 feet (1341 m) elevation near Empire City, NV (Jones, June 19, 1882, Intermountain Herbarium, Utah State University).

Flowering may occur when plants are as young as 2 years old. This species, however, ordinarily blooms in the fourth or fifth growing season. This average age of first flowering was determined from a survey by making ring counts of many young plants that had only 1 to 2 flower stalks, and which obviously had not flowered previously because there were no persistent spines on them.

Root Growth and Development

Budsage has a short thick vertical toproot up to 15 cm long, with many small horizontal branches. New root growth in budsage was first observed on plants that broke summer dormancy by late August 1963. The new rootlets were produced from the short taproot and from the larger horizontal branches. The newest roots were very succulent and whitish in color. The more mature new roots were somewhat woody and brown in color.

Table 4 reports the total length of new root growth that occurred in three trenches dug along one side of three plants at site 1. The period of growth was from August 23 to December 1, 1963. Even though this sample is only a part of the roots of the whole plant, it does point out that a considerable amount of root growth will occur when there is adequate later summer moisture.

The new roots produced were found in the top 30.5 cm of soil-- principally at the 15 cm level. One of the plants that was dug up had a new root that was at least 45.75 cm long. It grew across the trench through the disturbed soil in a horizontal direction at 15 cm below the ground surface.

Further examinations in February 1964 and June 1964 indicated that root growth continued at a low slow rate from December 1963 to February 1964 and then the rate increased from February to June. There are no comparable data for June because badgers dug up the plants. Nevertheless, in June water became a limiting factor and root growth ceased that growing season. Most of the roots grew in the top 7.6 to 17.8 cm of soil at both locations.

Table 4.--Amount of new root growth produced (August 23, 1963 to December 1, 1963) by three *A. spinescens* plants

Plant	Total length of succulent roots		Total length of brown roots		Total	
	inches	cm	inches	cm	inches	cm
A	66.25	168.3	24.50	26.2	90.75	230.5
B	38.50	97.8	--	--	38.50	97.8
C	21.50	54.6	89.00	226.1	110.50	280.7

Occasionally budsage produces adventitious roots. This occurs when the lowest branches are completely covered by soil. Plants growing in the bottomlands produced adventitious roots more often than those growing on benches.

The taproot of seedlings does not grow much deeper than 5 inches (12.7 cm) during the first year (fig. 4), and then lateral branchlets are produced (fig 5). As the plants mature, the taproot becomes much branched (fig. 6). The root systems shown are not complete, but show the relative amount of branching, rather than the total length of growth away from the taproot.

Roots of budsage are commonly found in the top 38.1-50.8 cm of soil and may be as shallow as 2.5-7.6 cm deep. Roots grow out in a horizontal direction as much as 1 m and as deep as 1.1 m. Horizontal branch roots as long as 2.1 m have been observed. Depth of soil, soil texture (which includes the amount of gravel present), and depths to which moisture penetrates seem to be the primary physical factors that determine the depth of penetration and distribution of the roots of budsage.

The roots of this species are much more branched and more thoroughly interpenetrate the soil than its associated shrub species. Such a highly branched root system allows budsage to take advantage of the limited spring soil moisture supply before the summer drought comes.

Budsage evades summer drought, yet it is able to take advantage of late summer rains and break dormancy. It is well distributed, but its relatively shallow root system is probably the key to adaptation to drought conditions and an

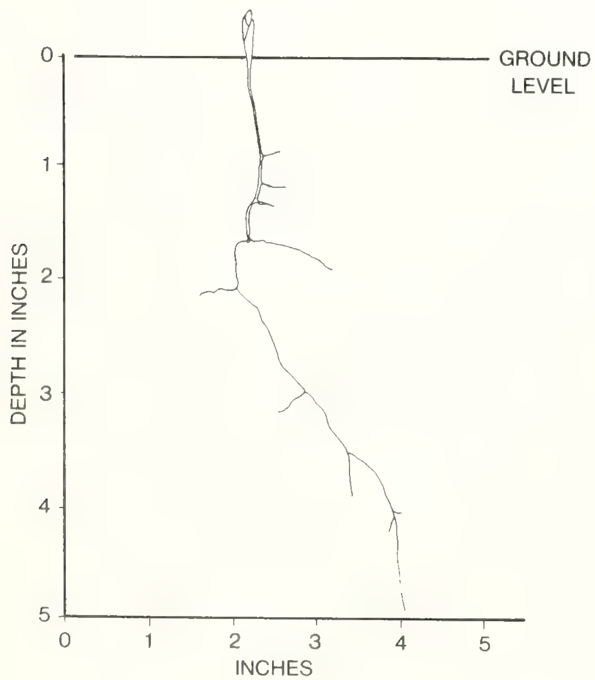


Figure 4.--*Artemisia spinescens* plant 26 days old. Seed was collected and planted June 11, 1964.

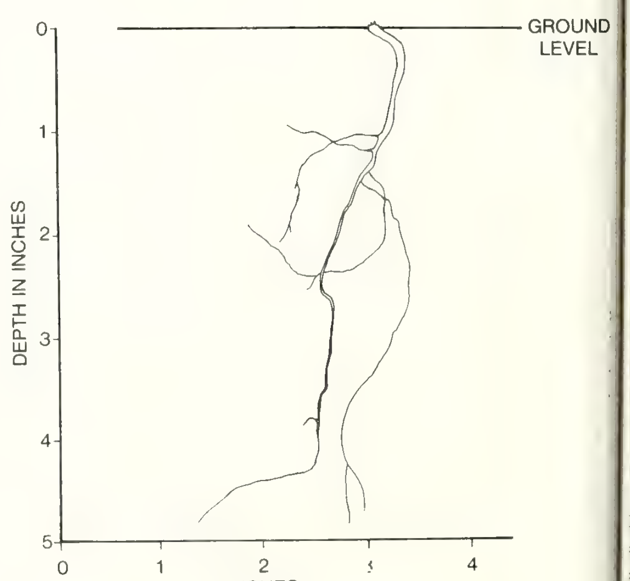


Figure 5.--Root system of a 1-year-old *A. spinescens* seedling.

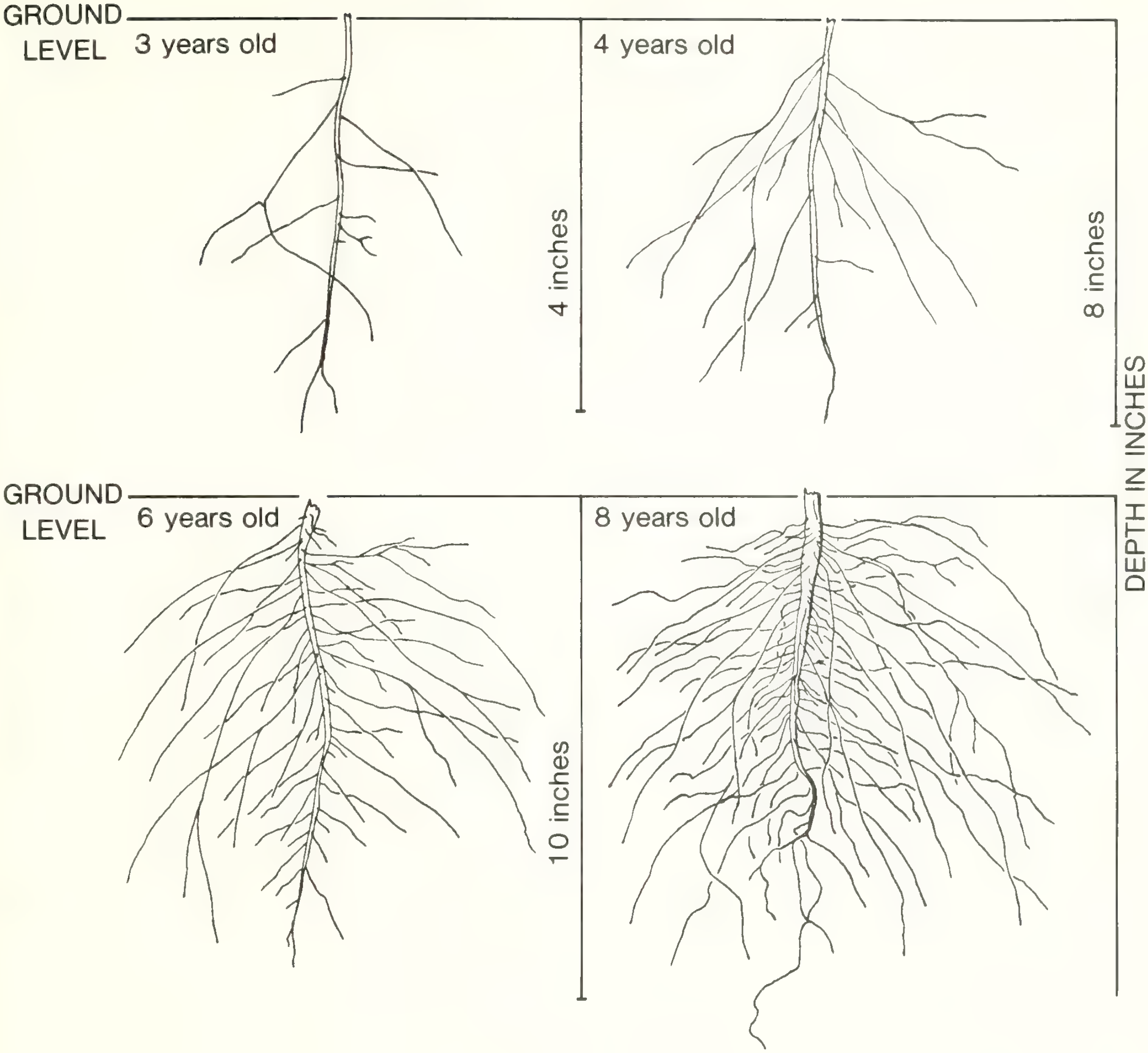


Figure 6.--Development of a much-branched root system on A. spinescens plants. Age was determined by counting annual rings.

ability to break dormancy when adequate moisture is present. Consequently, this species is able to taken advantage of summer moisture, but if moisture does not come, budsage is not seriously affected because it is dormant. If late summer rains do come, it does not put out an expanse of transpiring leaves. Substantial amounts of growth, however, can occur in the root system.

During those months in which growth conditions are suboptimum, only the small leaves and twigs are photosynthetic. Active growth takes place only when there is a more dependable supply of moisture in the spring and when evaporation is low.

Longevity of Budsage

It is difficult to obtain accurate ring counts on budsage because the center of the stem and root has usually rotted or has been eaten by boring insects. A lobing habit multiplies this difficulty of counting rings. In advanced age, the lobes separate and form a decumbent or nearly prostrate collection of stem segments (fig. 7).

Figure 7.--Artemisia spinescens that has separated into three branches.

Stem diameter is not necessarily proportional to age. From field observations it was found that large, rapid growing bushes reach an early maturity.

Plant counts of budsage on eight, 100-ft^2 charting quadrats in each of six experimental pastures of the DER indicated some plants were at least 29 years old. In the protected quadrats, out of 84 plants mapped in 1935 nearly one-fourth were still alive in 1964 (table 5). On the other hand, only 14 percent of the plants on the grazed quadrats were still present in 1964 (table 6).

Other observations on establishment of budsage in plots that contained no plants of this species in 1935 were made in pasture 16 which is grazed moderately in early winter. From 1935 to 1964, budsage became established at the rate of 23 plants per 400 ft^2 (37.2 m^2) in the protected enclosures and 3 plants per 400 ft^2 on the grazed areas. The lower establishment on the grazed plots can probably be attributed to preferential heavy use of individual plants. Effects of grazing on establishment are discussed later in this paper.

Table 5.--Number of *A. spinescens* plants that had become established since 1936, and were still aliv in 1964. Grazing intensity was judged as follows: light = 10 sheep days per acre; moderat = 14 sheep days per acre; heavy = 17 sheep days per acre

	Season of use			
	Midwinter		Late winter	
Grazing intensity	Protected	Grazed	Protected	Grazed
Light	34	2	5	0
Moderate	17	21	2	1
Heavy[1]	26	13	11	0
Totals	77	36	18	1

[1]Number of plants per four 100-ft^2 (9.3-m) charting quadrats; the other data are plants per eight quadrats.

Table 6.--Survival of individual *A. spinescens* plants from 1935 to 1964. Grazing intensity was judged as follows: light = 10 sheep days per acre; moderate = 14 sheep days per acre; heavy = 17 sheep days per acre

	Protected		Grazed	
Grazing intensity	No. plants present in 1935	No. original plants still present-1964	No. plants present in 1935	No. original plants still present-1964
		Grazed in midwinter		
Light	4	0	12	2
Moderate	8	2	20	4
Heavy	24	3	13	0
Totals	36	5	45	6
Percent survival		13.9		13.3
		Grazed in late winter		
Light	29	8	35	6
Moderate	17	5	22	3
Heavy[1]	2	2	3	0
Totals	48	15	60	9
Percent survival		31.5		15.0

[1]Number of plants per four 100-ft^2 (9.3-m) charting quadrats; the other data are plants per eight quadrats.

Effect of Clipping

At each of six sites, ten 200-ft^2 plots were randomly selected. In August 1963, current annual growth was estimated than clipped on five plots and estimated only on the remaining plots. In August 1964, all plots of the ten were clipped.

All of the plants clipped in 1963 had noticeable dieback on the clipped twigs. These dead areas extended 3 to 13 mm below the part of the stem which had been clipped. At the base of the dieback, from one to five, but ordinarily two, new lateral twigs were produced from latent, lateral buds. Almost all of the clipped plants produced more lateral vegetative twigs than those that were not clipped.

Because the current year's growth was clipped off, most of the buds which would have produced flowers in 1964 were also removed. Consequently, the clipped plants produced very few flowers in 1964. The flowers that were produced on the clipped plants came from flower buds located at the very base of the previous season's growth that were missed in twig removal. No latent reproductive buds were observed on stems older than the current year's growth.

Data regarding the effects of clipping are presented in table 7. In every case there was an increase in the number of twigs per plant from 1963 to 1964. This increase was greater on the clipped plants than on the nonclipped plants. The length of the twigs produced in 1964 was generally longer on the clipped plants. Only at site 7 was the length of the twigs on clipped plants shorter in 1964.

The plants from the protected site showed that the clipping in 1963 stimulated a small increase in herbage yield. The plants on the sites grazed by sheep and cattle had variable response. The data, however, show that the clipped plots produced more vegetative growth than the plots that were not clipped. Wherever there was a decrease, the decrease on the unclipped plots was greater than on the clipped; wherever there was an increase, the increase on the clipped plots was greater than on the unclipped.

One possible reason for this increase, even though the clipping was severe, is that the clipping removed essentially all of the reproductive potential; consequently, the plants were forced to produce only vegetative growth. It is not known how long the plants could withstand such severe clipping or grazing. These and other observations suggest that repeated heavy grazing may kill budsage quite rapidly.

Table 7.--Effect of clipping on _A. spinescens_. Average precipitation for October 1962 to May 1963 was 3.50 inches; for October 1963 to May 1964, 4.09 inches (Average for October to May period was 3.76 inches)

Sites	Treatment	Average number of twigs per plant		Average twig length (inches)		Productivity		
						Grams/1000 ft^2		Percent change
		1963	1964	1963	1964	1963	1964	1963 to 1964
Protected:								
Ungrazed area	clipped	33.4	124.4	0.5	0.8	120	140	+17
(site 1)	control	30.1	69.5	0.5	0.7	180	87	-52
Grazed by sheep:								
Allotment No. 3	clipped	28.7	57.7	1.0	0.7	60	70	+17
(site 7)	control	22.0	40.5	0.5	1.2	65	60	-8
Allotment No. 2	clipped	19.9	42.6	0.5	0.8	125	172	+38
(site 8)	control	15.3	31.7	0.4	0.8	135	170	+26
Grazed by cattle:								
Burbank Junction	clipped	45.3	79.9	0.4	0.9	316	304	-6
(site 4)	control	38.7	38.9	0.8	0.8	280	172	-39
Lower Pine Valley	clipped	45.2	147.5	0.5	1.5	132	280	+112
(site 5)	control	46.8	78.5	0.7	1.4	175	202	+15
Hamlin Valley	clipped	--	--	--	--	386	380	-2
(site 6)	control	--	--	--	--	375	215	-43

EFFECTS OF GRAZING

Ratio of Spine to Vegetative Twigs

In 1964 and 1965 plants were chosen and their current year's vegetative twigs and current year's spines were counted. A spine/ vegetative twig ratio was then computed. These data were obtained from a protected area, from moderately winter grazed DER pastures and from a heavily winter grazed allotment. Table 8 presents the total number of vegetative twigs and spines counted on the plants and the computed ratios. Even though these data do not represent clearcut interactions between grazing and plant growth because the effects of climate, specifically precipitation, are included, they do indicate that heavy grazing and late winter grazing adversely affect production of vegetative twigs and spines, respectively.

These data also indicate that some grazing in midwinter may actually stimulate growth of twigs, which become spines. This observation is proposed because the number of spines produced in 1964 and 1965 under moderate midwinter grazing did not change.

The apparent difference in the spine/twig ratios of plants under moderate grazing can probably be explained on the basis of herding. Sheep in a pasture tend to be more confined, thus graze preferred species more repeatedly than those in an allotment, which is more like being on open range.

The large decrease in the spine/vegetative twig ratio in the enclosure was probably related to plant vigor. These plants were rather large and symmetrical compared to the grazed plants. The grazed plants had branches with varying lengths and numbers of buds, and therefore had less variation in the spine/twig ratio, except under the heavy grazing regime.

Each year all of the flower buds elongate and few, if any remain latent. When the plants are grazed or clipped, they produce mostly vegetative growth from latent buds on stems older than the current year's growth. Normally fewer flower stalks were observed per plant in areas grazed by sheep than in areas grazed by cattle or in protected areas.

The effects of grazing on plant establishment are reported in Table 5. Plant establishment appeared directly affected by season of grazing but not by the intensity of grazing.

Cover of _A. spinescens_

On the DER, budsage is present in moderate amounts in most of the plant communities (tables 9 and 10). The period of grazing on this species is shorter, and the amount of herbage it produces is less than that of the associated shrubs. The percentage utilization on budsage is highest during the late winter (Hutchings and Stewart 1953). During February and March, it usually is one of the principal shrubs browsed by sheep. Nevertheless, this species does not

Table 8.--Spine:vegetative ratio of plants under protection and grazed moderately and heavily

Grazing	Vegetative twigs per plant		Spines per plant		Spines:twigs	
	1964	1965	1964	1965	1964	1965
A. Moderate[1]						
Midwinter season						
DER Allotment No. 2, Unit No. 2	22.0	27.6	27.0	32.4	1.23	1.17
DER Pasture 2	27.5	34.5	17.7	18.1	0.64	0.52
Mid - late winter season						
Pasture 6	31.9	48.4	76.0	24.9	2.38	0.51
B. Heavy[2]						
All winter season						
Antelope Valley - BLM Rangeland	25.4	20.7	18.0	9.7	0.71	0.47
C. Protected						
Enclosure in DER Pasture 2	38.3	40.1	87.2	43.9	2.28	1.09

[1] Moderate = 53% utilization of herbage produced the previous summer (14 sheep-days per acre).

[2] Heavy = 68% utilization of herbage produced the previous summer (17 sheep-days per acre).

Table 9.--Cover data for six desert communities. Site No. 5 was evaluated using the line-point method which is a modification of the point-frame method of Levy and Madden (1933). The other communities were evaluated using the line-intercept method (Canfield 1941). Six 100-foot (30.5 m) transects were used at each location "T" = 1% cover

Site factor	Site number					
	1	2	3	4	5	6
	% cover					
Bare soil	66	81	77	56	74	82
Litter	16	6	8	20	11	--
Vegetation	19	13	15	24	15	18
	% composition					
Artemisia spinescens	9	51	26	28	10	75
Ceratoides lanata	15	49	T	--	T	25
Atriplex confertifolia	13	--	59	8	29	--
Chrysothamnus viscidiflorus ssp. *stenophyllus*	10	--	--	--	--	T
Sarcobatus vermiculatus	--	--	--	64	--	--
Opuntia sp.	--	--	--	--	T	--
Ephedra nevadensis	--	--	2	--	--	--
Oryzopsis hymenoides	11	--	2	--	5	--
Hilaria jamesii	10	--	--	--	12	--
Sporobolus cryptandrus	--	--	T	--	--	--
Aristida fendleriana	1	--	--	--	--	--
Bromus tectorum	--	--	T	--	--	--
Sphaeralcea glossulariaefolia	T	T	T	--	--	T
Salsola iberica	30	--	--	--	44	--
Aster sp.	1	--	T	--	--	--
Lappula redowski	--	--	T	--	--	--
Halogeton glomerata	T	--	5	T	--	--
Astragalus lentiginosus	--	--	--	--	T	--

Table 10.--Plant density of five desert communities. Values represent numbers of plants per square meter. p = present but not counted

Species	Site number					
	1	2	3	4	5	6
Artemisia spinescens	2.4	21.6	9.7		1.6	35.2
Ceratoides lanata	5.6	33.9	0.2		0.1	31.5
Atriplex confertifolia	2.8	--	21.6		3.4	--
Chrysothamnus viscidiflorus ssp. *stenophyllus*	0.9	--	0.1		--	0.3
Opuntia sp.	--	--	--		0.6	--
Tetradymia spinosa	--	--	--		0.1	--
Xanthocephalum sarothoae	--	--	--		3.3	--
Oryzopsis hymenoides	2.3	--	0.5		48.9	--
Hilaria jamesii	17.8	--	--		--	--
Sporobolus cryptandrus	--	--	p		--	--
Aristida fendleriana	0.1	--	0.1		0.2	--
Sphaeralcea glossulariaefolia	--	--	0.8		0.1	--
Salsola iberica	p	--	0.8		14.9	--
Aster sp.	1.3	--	--		--	--
Halogeton glomerata	--	--	p		0.6	--
Astragalus lentiginosus	--	--	--		1.0	--

constitute a large portion of the sheep's diet, because it is usually a minor constituent of the available forage. In most of the communities in which it occurs, budsage is less than 20 percent of the total cover. However, it does constitute an important portion of the forage, especially in years when it breaks dormancy in late summer or fall. As pointed out earlier, in the 1963-64 and 1965-66 grazing seasons, it was grazed through the entire winter season at the DER. Sheep graze the growth of the preceeding season on the erect and easily obtainable twigs and the green foliage as it expands and grows in the early spring. If this species is the only one to begin growth in early spring, it is preferentially grazed and probably grazed rather heavily.

The relative amount of shrubs contributing to the total cover was markedly higher in 1964 than in 1935 in the enclosures and adjacent grazed areas except those which were heavily grazed (table 11). In each of the enclosures, there has been a marked increase in budsage with a simultaneous decrease of shadscale. In pastures 11 and 12, budsage increased from about one-fifth to about one-half of the shrub cover. This represents an actual increase from 8.4 to 44.0 percent of the total plant cover for pastures 11 and 12, respectively. This same trend also occurred in the enclosures of pastures 10 and 15 (Holmgren and Hutchings 1972).

The trends in cover composition of budsage with respect to grazing by sheep indicate that season of grazing is more important than intensity of grazing. This is because this species ordinarily does not slip until late winter, and therefore, is usually not grazed until then. Regardless of grazing intensity in midwinter, its cover composition did not change from 1935 to 1964 (Holmgren and Hutchings 1972). On the other hand, under light grazing in late winter, budsage decreased from 12.9 to 3.9 percent of the total plant cover. Heavy grazing in late winter has almost eliminated this species, while winterfat remained almost constant. Additional evaluations by Holmgren and Hutchings (1972) show winterfat has actually decreased under late winter, heavy grazing. Because of its high palatability, especially in late winter, budsage is one of the first plants to be affected by heavy grazing.

Density of Budsage

The effects of grazing by season on the density of budsage and three associated species are presented in figures 8 and 9. In all of the protected areas, there is a trend of shrubs increasing at the expense of Indian ricegrass. In general, the density of budsage increased or remained essentially the same. Where winterfat was present in large numbers, it decreased in the ungrazed enclosures from 1936 to 1964; where winterfat was present in low numbers, it increased.

Light grazing in midwinter at pasture 11 allowed budsage to increase somewhat, but the increase was not as great as that in the enclosure. Budsage and winterfat decreased and shadscale and Indian ricegrass increased at pasture 2, which is grazed moderately in midwinter. In pasture 12, which is heavily grazing in midwinter, budsage, shadscale, and Indian ricegrass decreased, whereas winterfat increased.

Table 11.--Percentage change of A. spinescens numbers from 1936 to 1964 on protected and grazed plots. Plant counts were made on 80 200-square-foot plots in each treatment at each site. Grazing intensities were judged as follows: light = 10 sheep days per acre; moderate = 14 sheep days per acre; heavy = 17 sheep days per acre

Grazing intensity and season	DER pasture	Protection 1936	Protection 1964	Protection % change	Grazed 1936	Grazed 1964	Grazed % change
Light:							
Midwinter	11	301	746	+134	335	520	+55
Late winter	10	1007	1007	-11	831	187	-77
Moderate:							
Midwinter	2	254	953	+275	557	277	-52
Late winter	6	775	807	+4	698	161	-77
Heavy:							
Midwinter	12	495	1286	+160	663	677	+0.6
Late winter	15	274	892	+225	396	48	-88

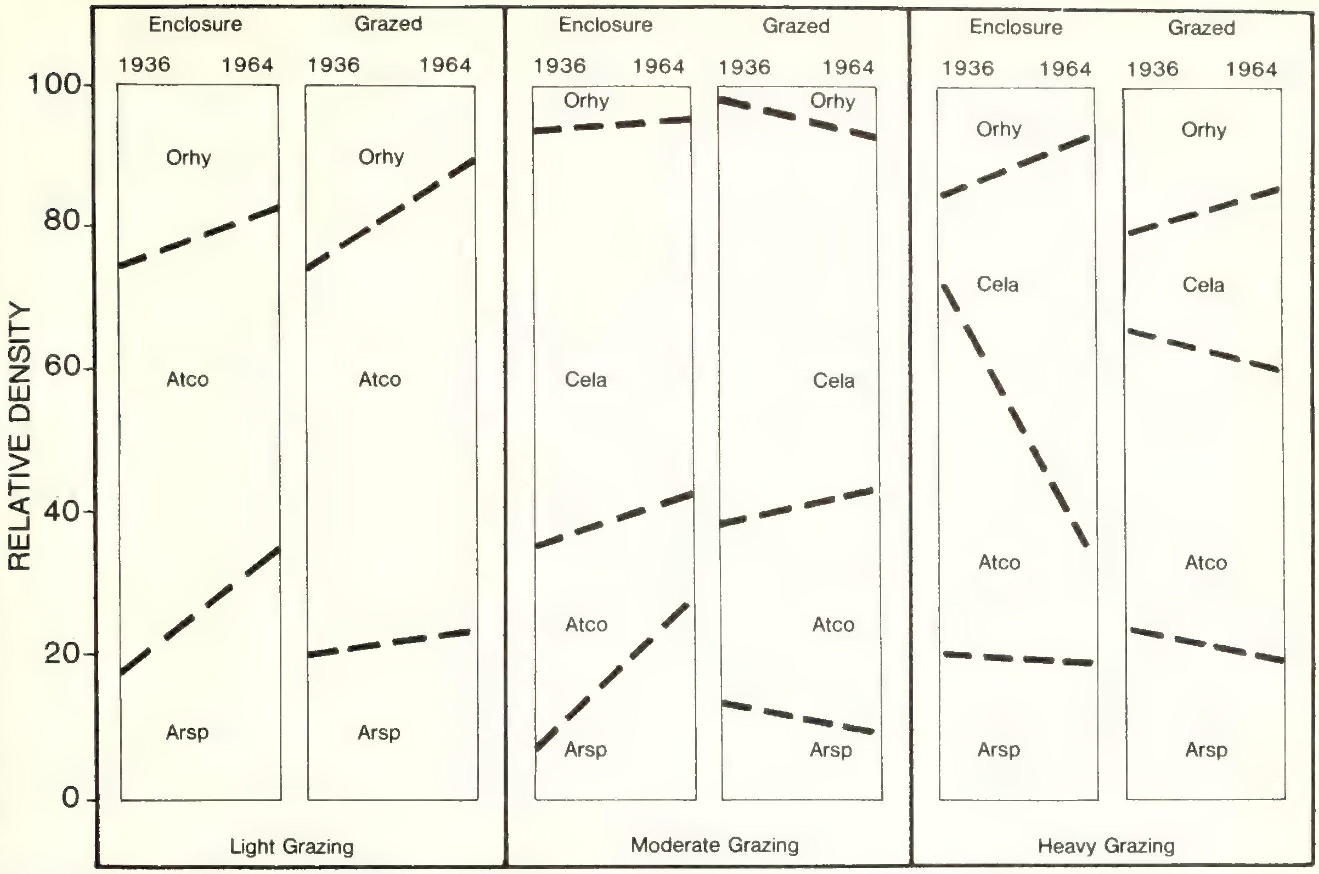


Figure 8.--Effects of midwinter grazing on relative density of A. spinescens, Atco - Atriplex confertifolia, Cela = Ceratoides lanata, and Orhy = Oryzopsis hymenoides.

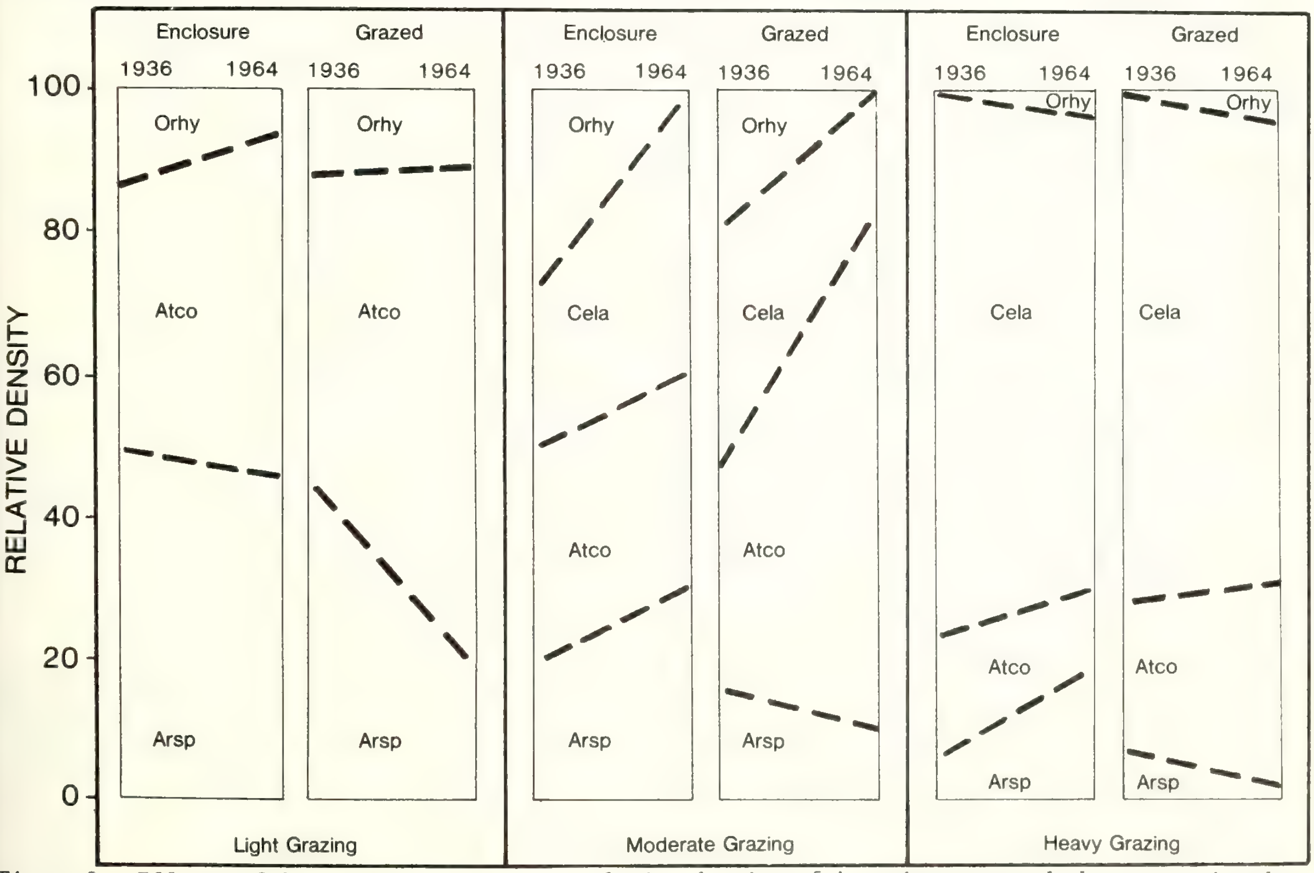


Figure 9.--Effects of late winter grazing on relative density of A. spinescens and three associated perennial species. Arsp = A. spinescens, Atco = Atriplex confertifolia, Cela = Ceratoides lanata, and Orhy = Oryzopsis hymenoides.

Grazing in late winter decreased both budsage and winterfat resulting in a corresponding increase in shadscale. The decrease of budsage under both heavy and moderate grazing was approximately the same, 5 percent. However, pasture 15, the more heavily grazed pasture, had only a small amount of budsage to begin with, and heavy grazing at this site has almost eliminated it. On the other hand, light grazing at pasture 10 has also severely decreased this species. Because pasture 10 is dominated by only two shrub species, budsage is preferentially grazed detrimentally. This is not the case in pastures 6 and 15, even though they are grazed moderately and heavily, respectively, because winterfat is present in those two pastures and it receives some of the grazing pressure budsage would otherwise receive. Shadscale, the least palatable species, increased under any grazing intensity during late winter.

Figures 8 and 9 also show that the grazed acres under all six treatments have deteriorated. In no case is variety of species as good as it was 28 years earlier. The percentage change of the number of budsage plants from 1936 to 1964 is reported in table 11.

The same trends, budsage increasing under protection or light grazing in midwinter and decreasing when grazed in late winter, were also observed on a range allotment of the DER as well as the open range. In these areas, field observations indicate that where budsage is common, it is preferentially and rather heavily grazed in late winter until other plants such as forbs, grasses, and winterfat begin to grow. In order to maintain these areas, sheep must not be allowed to remain too long.

It is generally accepted that change in composition of dominant palatable and unpalatable species is a function of grazing pressure. Norton (1978) studied many of the same plots from which the cover and density data presented here were taken, and after considering all species concluded there is a general lack of difference between survival of grazed and ungrazed populations. Norton (1978) also concluded there are only small differences in the vegetation and its changes under different intensities of use. The above conclusions were based on evaluations comparing grazed and ungrazed populations without pointing out the interactions of season and intensity of grazing that have particular application in the case of budsage.

Figure 10 illustrates a comparison between site 2, which is moderately grazed in midwinter every other year, and the adjacent heavily grazed open range. The stand within the fence is 51 percent budsage and 46 percent winterfat by cover. The stand on the open range is almost 100 percent winterfat. Heavy grazing has essentially eliminated budsage.

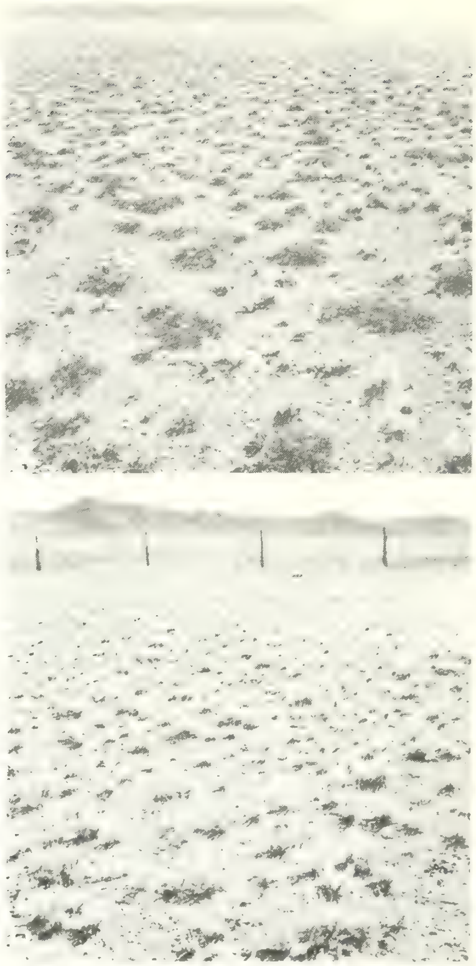


Figure 10.--Comparison of adjacent moderate and heavily grazed areas. Vegetation in the moderately grazed area (A) is an A. spinescens C. lanata stand; that of the heavily grazed are (B) is almost a pure stand of C. lanata. Photo correspond to site 3 in table 1. The dark plants in photo "A" are A. spinescens and the light ones are C. lanata.

Heavily grazed plants become hedged and grow close to the ground. These plants may never produce flowers at all; consequently, seedlings are rare. The budsage plants in the open range allotments are small hedged plants. In those areas that were not grazed during the 1962-63 grazing season, most of the plants produced onl a few flower stalks. However, in 1963, hardly any plants produced even one flower stalk because nearly every twig of the 1963 growing season had been grazed off short enough to remove reproductive buds.

The combination of the effects of grazing and climate tend to produce stands of budsage which are even aged, or that have only two or three age classes. The stands are also generally of the same size and state of vigor. Only in protected areas or in areas having mixed shrubs

and grasses are there plants of all ages, size classes, and different states of vigor. Protected plants are not as bushy as those that are lightly or moderately grazed. Even light grazing was found to break apical dominance allowing more lateral buds to elongate. Consequently, lightly grazed plants tend to be more rounded with the larger branches having more lateral bud development.

ACKNOWLEDGEMENTS

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CYTOGEOGRAPHY OF CHRYSOTHAMNUS VISCIDIFLORUS

Loran C. Anderson

\BSTRACT: Polyploidy in Chrysothamnus
Asteraceae) is restricted to three of the five
ubspecies of C. viscidiflorus. Comparisons
etween the diploids and polyploids are made for
ach subspecies. Geographical and climatologi-
al correlations show that polyploids in each
ase seem to be adapted to warmer, usually drier
ites than their diploid counterparts.
ronically, the two subspecies known only as
iploids also occur in the warmer, drier parts
f the species' range.

NTRODUCTION

hromosome numbers have been determined for early 500 populations representing all taxa of hrysothamnus. Polyploidy is restricted to C. iscidiflorus (Hook.) Nutt. All other species re basically diploid with x = 9. Rarely, an ndividual in a diploid population has been hown to be tetraploid, or a few cells in a iploid plant are polyploid.

hrysothamnus viscidiflorus has five subspecies. he ssp. axillaris (Keck) L.C. Anderson and ssp. lanifolius L.C. Anderson are known only as iploids (2x). Subspecies lanceolatus (Nutt.) all & Clem. and ssp. puberulus (D.C. Eaton) all & Clem. have both 2x and 4x populations, hereas ssp. viscidiflorus has 2x, 3x, 4x, 5x, nd 6x plants (the notation 2n, 3n, 4n, etc., is sed in the figures). The triploid and penta- loid plants (one each) were atypical in ppearance.

he polyploids are mostly autopolyploids Anderson 1966) although allopolyploids (the erm used here in a very narrow sense) derived rom ssp. lanceolatus and ssp. viscidiflorus ccur sporadically from northern Colorado to ortheastern Nevada.

hrysothamnus viscidiflorus is wide-ranging and as great ecological amplitude. Geographical nd climatological data are compared with plant orphology and ploidy levels in an attempt to nderstand further the biology and taxonomy of ne species.

ETHODS

hromosome counts for the 238 samples of ssp. anceolatus, ssp. puberulus, and ssp. viscidiflorus used in this study have already been recorded (Anderson 1966, 1971; Anderson and others 1974). Measurements of vegetative and floral features were taken as in Anderson (1964).

Altitude and latitude were determined for each collection. Mean annual temperature and mean annual precipitation were obtained mostly from U. S. Weather Bureau documents. Data for more remote collection sites were supplied by state climatologists, but precipitation data for a few collections were not available.

Statistical studies of the plant and environmental data included multivariate analysis and Wilk's Lambda test.

RESULTS

Analysis of Polyploid Subspecies

C. v. ssp. lanceolatus.--This subspecies ranges from southern British Columbia to northern New Mexico. Specimens of diploids used in this study came from latitudes of 38°12'N. to 47°24'N. and occurred from 976 to 11,000 ft (297-3353 m) in elevation. The tetraploids studied had a greater range (36°0'N. to 49°02'N.) and came from 800 to 8,500 ft (243-2590 m) in elevation. Mean latitude and altitude are given for each ploidy level in table 1. Mean annual climatological data are also given.

Table 1.--Means for selected environmental and morphological data for C. v. ssp. lanceolatus. Features that are significantly different (1 percent level) are underscored

Feature	2x	4x
Latitude	41°11'N.	41°58'N.
Altitude (ft)	7,139.3	5,745.5
Annual temperature (°F)	38.01	43.68
Annual precipitation (in)	17.80	13.82
Leaf width (mm)	3.18	3.11
Leaf width/length	0.106	0.111
Involucral length (mm)	6.60	7.43
Corolla length (mm)	5.19	5.56

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Diploids have slightly longer, relatively narrower leaves than tetraploids, but the differences are not significant. The relatively shorter involucres and corollas of the diploids are significantly different when mean lengths are considered (table 1). However, sufficient overlap in size occurs to preclude use of such measurements to determine ploidy level of plants in the field. Other floral features were measured and statistically analyzed for each group but were not sufficiently interesting to record here.

C. v. ssp. puberulus.--This subspecies is largely a plant of the Great Basin. It was probably derived phylogenetically from ssp. lanceolatus. Specimens of diploids used in the study came from latitudes from 36°54'N. to 41°12'N. and from altitudes of 4,200 to 10,000 ft (1280-3048 m). The tetraploids studied have a narrower range in south-central Nevada and adjacent California at 36°30' to 38°06' north latitude; they occurred from 5,200 to 8,100 ft (1585-2467 m) in elevation. Mean latitude and altitude data are given in table 2. In that portion of the subspecies' range where both diploids and tetraploids occur, the tetraploids are at higher elevations. The tetraploids generally receive warmer weather and more precipitation than the diploids, but the differences are not statistically different.

Table 2.--Means for selected environmental and morphological data for C. v. ssp. puberulus. Features that are significantly different (1 percent level) are underscored

Feature	2x	4x
Latitude	38°39'N.	37°10'N.
Altitude (ft)	6,085.9	6,795.6
Annual temperature (°F)	47.42	48.07
Annual precipitation (in)	8.65	9.84
Leaf width (mm)	1.32	1.76
Leaf width/length	0.078	0.119
Involucral length (mm)	5.87	7.10
Corolla length (mm)	5.11	5.25

Diploids have generally shorter, relatively narrower leaves than the tetraploids. The diploids also have shorter involucres, but corolla lengths are not distinctive between the two groups.

C. v. ssp. viscidiflorus.--This subspecies is one of the most widespread taxa in the genus. It ranges from northern Washington, western Montana, and northwestern Nebraska to southern California and northern Arizona. It occurs in a wide variety of habitats, and the few soils that have been tested range in pH from 6.0 to 8.4

Specimens of diploids used in this study came from latitudes from 34°18'N. to 47°19'N. and from altitudes of 850 to 12,800 ft (259-3901 m). Tetraploids occurred, generally, but not exclusively, in more southern latitudes (35°05'N. to 46°18'N) and at altitudes of 960 to 10,300 ft (283-3139 m). In mountains of southern California, the southern limits of the subspecies' range, diploids occur, but in deserts of northern Arizona only tetraploids occur. At any given latitude where both occur, the tetraploids are generally at lower elevations than the diploids (fig. 1). But in northeastern Nevada and in eastern Washington the two ploidy forms can occur in mixed populations.

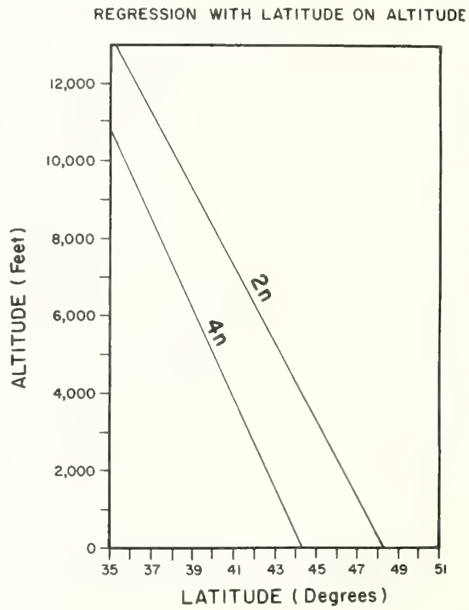
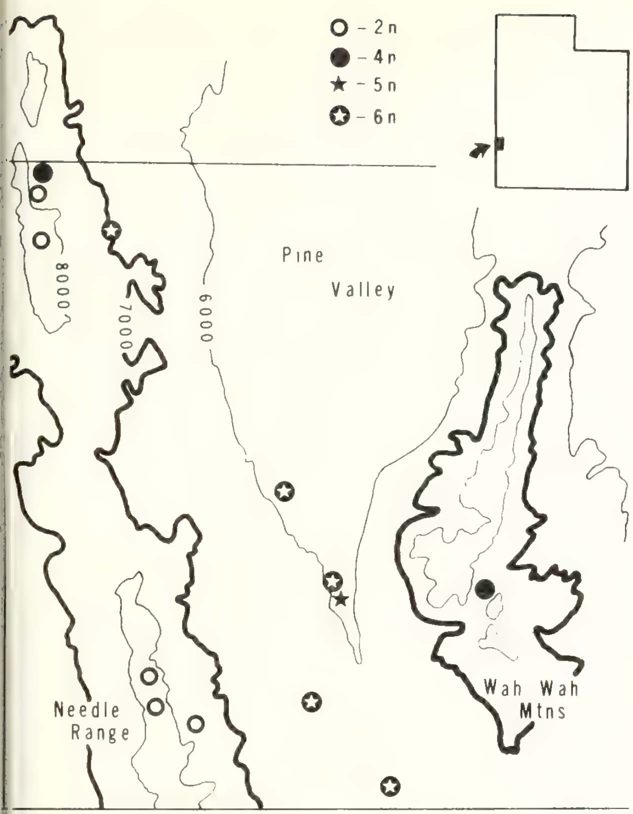


Figure 1.--Geographical relationships of cytotypes of C. v. ssp. viscidiflorus.

The hexaploids of the subspecies occur sporadically from southwestern Utah through south-central Nevada at latitudes of 37°06'N. to 39°12'N. and at elevations from 5,100 to 7,000 ft (1554-2133 m). Mean latitudinal differences among the three ploidy levels are significantly different. An excellent example of altitudinal and climatological zonation among the different ploidy levels is found on the Desert Experimental Range in southwestern Utah (fig. 2). The hexaploids occur in the Pine Valley desert mostly below 7,000 ft (2133 m) in areas that receive about 5.5-11 inches (14-28 cm) precipitation annually. The tetraploids are in the pinyon-juniper zones of the Needle Range and Wah Wah Mountains around 7,500 ft (2286 m) in elevation and receive about 12.5-13.2 inches (32-34 cm) of precipitation annually. Diploids



igure 2.--Elevational distribution of ssp. iscidiflorus cytotypes in southwestern Utah elevations in feet).

enerally occur above 8,000 ft (2438 m) in the eedle Range and receive 15-17.5 inches (38-44 n of precipitation annually.
ean climatological data for all samples of this ibspecies (table 3) show that diploids occur on ie coolest and wettest (highest elevation) tes, whereas the hexaploids occur on the hot-est and driest sites, with the tetraploids eing intermediate.

ie three major ploidy levels in subspecies scidiflorus (2x, 4x, 6x) are not readily stinguishable in the field based upon morpho-gical characteristics. However, measurements om all samples show that the mean leaf width id mean involucral and corolla lengths are gnificantly different for the three (table 3). 1 general, polyploids have increased cell size ewis 1980) and may show increased plant size ien compared to diploids. The pattern is evi-nt in involucral and corolla lengths--ivolucres and corollas of tetraploids are nger than those of diploids, and those of xaploids are longer than those of traploids. The trend for increased size is t maintained in foliar features. Although the traploids have somewhat wider leaves than the ploids, the hexaploids have the narrowest aves.

Table 3.--Means for selected environmental and morphological data for _C. v._ ssp. _viscidiflorus_. Features that are significantly different (1 percent level) are underscored

Feature	2x	4x	6x
Latitude	40°49'N.	38°53'N.	37°53'N.
Altitude (ft)	6,236.1	6,335.6	6,031.0
Annual temperature (°F)	43.75	46.86	46.45
Annual precip. (in)	13.50	12.31	7.36
Leaf width (mm)	2.42	2.91	2.29
Leaf width/length	0.073	0.078	0.066
Involucral length (mm)	6.58	7.22	8.13
Corolla length (mm)	4.97	5.49	5.67

Ploidy Level Sorting by Environmental Factors

Wilk's Lambda test was applied to the multi-variate discriminant analysis of the data to determine the significance of environmental factors in sorting the ploidy levels by environmental factors. For _C. v._ ssp. _lanceolatus_, the computer had 80 percent accuracy in correctly sorting the diploids and tetraploids by mean annual temperature alone (2x with low temperatures; 4x with high temperatures).

For _C. v._ ssp. _puberulus_, the computer had 81 percent accuracy in sorting by primarily using latitude, then altitude, and then precipitation (2x with high latitude and low altitude and precipitation; 4x with low altitude and high altitude and precipitation).

For _C. v._ ssp. _viscidiflorus_, the hexaploids were not considered because of small sample size. The computer had 67 percent accuracy in its discriminating power using latitude and temperature equally (2x with high latitude, low temperature; 4x with low latitude, high temperature).

Ploidy Level Sorting by Morphological Features

Wilk's Lambda test was also used to determine the significance of selected morphological features in sorting ploidy levels. For _C. v._ ssp. _lanceolatus_, the computer was not able to sort the different ploidy levels effectively. It showed no significant differences in the morphologies even though the means for floral features were significantly different (table 1).

For _C. v._ ssp. _puberulus_, there was strong correlation between morphological features and ploidy level. The computer correctly sorted the

ploidy levels 87 percent of the time using first leaf width, then corolla length, and finally involucral length (table 2).

For C. v. ssp. viscidiflorus, the hexaploids were again omitted because of small sample size. Correlations for the diploids and tetraploids were weak. The computer had 64 percent accuracy in sorting leaf width. Other variables were not significant.

DISCUSSION

Early research on polyploidy suggested that the distribution of polyploids was generally correlated with increases in latitude or altitude. More recent research has failed to confirm those hypotheses (Ehrendorfer 1980). Chrysothamnus analyses certainly do not support those earlier views. Figure 3 gives a schematic summary of the relationships of cytotypes to one another and to geography. Diploids of ssp. lanceolatus and, especially, ssp. viscidiflorus seem generally to occur at higher latitudes or altitudes. Their polyploid derivatives occur at lower latitudes or altitudes. A similar pattern in the same geographical region has been reported for Atriplex confertifolia by Stutz and Sanderson (1983).

In figure 3, the dotted lines show tetraploids derived from crossing between ssp. lanceolatus and ssp. viscidiflorus. The dashed line suggests that the Great Basin ssp. puberulus may have been derived from the Rocky Mountain ssp. lanceolatus. The exception to the general trend

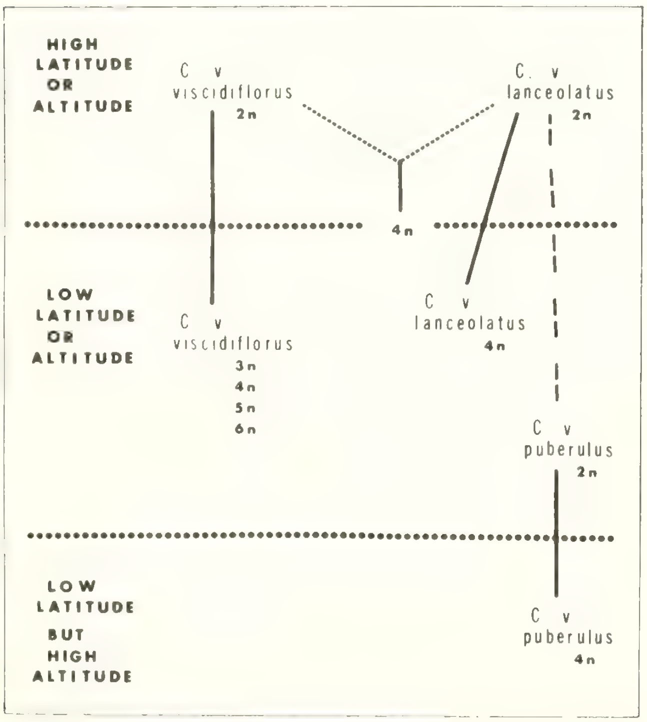


Figure 3.--Cytotype relationships in the polyploid subspecies of C. viscidiflorus.

in cytogeography in the species involves ssp. puberulus wherein the tetraploids occur at lower latitudes but at higher elevations.

Most of the lower latitudes of the Great Basin are those areas anciently covered by Lake Bonneville and Lake Lahontan. These areas represent the newer (and drier) habitats, and they are the sites largely inhabited by the polyploids of Chrysothamnus.

In an earlier study (Anderson and Fisher 1970), a numerical index of phylogenetic specialization was obtained for each taxon of Chrysothamnus based upon floral anatomy. Subspecies viscidiflorus with an index of 6.4 on a scale of 1 to 10 is thought to be the least specialized subspecies of C. viscidiflorus. The phylogenetic indicators may be applied to the data presented here. Subspecies puberulus is thought to be derived from ssp. lanceolatus. Diploid puberulus has a higher index (7.9) of specialization (i.e., is more advanced) than ssp. lanceolatus (7.6). The polyploids are clearly derived from the diploids in each subspecies. In each of the three subspecies, the tetraploids have slightly higher indexes than their diploid counterparts, which reinforces the presumed reliability of the floral indicators of specialization. Floral anatomy of hexaploids was not studied.

The preferential occurrence of polyploids of the three subspecies in the warmer, generally drier parts of the range of C. viscidiflorus is well documented here, but adaptation to those areas via polyploidy is not the only way. The ssp. axillaris and ssp. planifolius, which are known only as diploids, occur in the same warm, dry areas. Based on floral anatomy, the former has a relatively high index of specialization (8.0) but ssp. planifolius has an index of 7.3. Considering the entire genus, the diploid C. paniculatus occurs in the hottest, driest part of the genus's range, and that species has the highest index of specialization in the genus, 9.3.

ACKNOWLEDGMENTS

Ralph C. Holmgren is thanked for providing seed for chromosome counts and climatological data from the Desert Experimental Range. Nick Gotelli helped with statistical analyses. This work has been supported by a series of grants from the National Science Foundation, the most recent being DEB-8021776.

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SYMPATRIC SUBSPECIES IN CHRYSOTHAMNUS NAUSEOSUS

Loran C. Anderson

ABSTRACT: Chrysothamnus nauseosus (Asteraceae) is the most complex species in the genus. The 22 recognized subspecies are variously allopatric, parapatric, or sympatric. Tendencies for inbreeding enhance the sympatricity. Some sympatric units represent distant members of a ring of races but are interconnected through a series of other subspecies. Others appear to be reproductively isolated over much of their sympatric ranges, but the isolation breaks down at the edge of one of the subspecies' geographical and ecological range limit.

INTRODUCTION

In western America, C. nauseosus is the most widespread species in the genus and the most complex taxonomically. Hall recognized 22 varieties of C. nauseosus in 1919, and he noted the difficulty in assigning specific or varietal rank to all of the forms with the following:

> Nothing can be more certain than that these forty-two attempts to recognize species and varieties do not by any means exhaust the resources of the group. Every autumnal excursion into a new district brings to light one or more forms not previously described. The only limits set to the number of new species or varieties which might be set up lie in one's ability to visit all parts of the field during the flowering period and the failure or disinclination to recognize minute variations.

In 1923, Hall and Clements recognized 20 subspecies. Now 22 subspecies are recognized, although not the same entities listed by Hall in 1919 (Anderson overview paper, this proceedings).

The complexity in C. nauseosus prompted Feddema (in Voss 1981) to propose:

> The overwhelming need for simplicity and stability in nomenclatural practice by non-botanical scientists and land managers must be considered. We would be reluctant to invite a proliferation of names in such complex genera as Artemisia and Chrysothamnus which are of such practical importance in the Western United States.

Simplicity and stability in nomenclature can only truly be obtained in such a difficult species complex when the taxonomy most closely approaches the major patterns of variation that are present.

Diversity in C. nauseosus is apparently due to a nearly optimal combination of outbreeding and inbreeding (Anderson 1966, 1973). There are no indications of apomixis in the species (Anderson 1970). Several subspecies are generalists with fairly wide ecological amplitudes, but some subspecies are more narrowly adapted in habitat and range.

The need for so many names in C. nauseosus can be understood, in part, through an examination of distributional patterns. Many subspecies maintain their identities despite overlapping ranges because of their tendency toward inbreeding. The terms allopatric and sympatric are commonly used to describe spatial relationships between populations or taxa. In allopatry the taxa live in different areas; they may be disjunct or contiguous (in the latter case they are often termed parapatric). Sympatric taxa live in the same territory. Grant (1981) subdivides sympatry into neighboring sympatry, wherein taxa live in different niches in the same general habitat, and biotic sympatry, where taxa live in the same niches.

Tendencies for inbreeding in subspecies of C. nauseosus make it difficult to assess the degree to which they can interbreed (Anderson 1973, McArthur and others 1978). Therefore, introgression between taxa is inferred here based upon extensive field observations and herbarium studies coupled with reduced pollen fertilities in certain specimens. Distributional patterns in and interrelationships among the more widely distributed subspecies are discussed below.

OBSERVATIONS

Map 1. Subspecies albicaulis and Subspecies nauseosus

The subspecies are parapatric. Their morphologies are distinct, but the taxa intergrade

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reely through their narrow zone of contact in estern Montana and Wyoming. Such a distribuional pattern fits that of classical subspeies.

ap 2. Subspecies albicaulis and Subspecies ololeucus

he subspecies are largely allopatric, but their anges are adjacent in the Owens Valley of alifornia and overlap in southwestern Idaho and entral Utah. They are separate morphologically xcept in Utah where intergradation is evident. t should be noted that not all Utah specimens epresent intergradants. Subspecies albicaulis ccurs in the higher mountains and ssp. holoeucus occupies the basins. The two intergrade t the lower elevations in the mountains of tah, but not in Idaho or in Owens Valley. opulations in the Spring Mountains of southern evada and Clark Mountain of adjacent California epresent intergradants of these two subspecies.

ap 3. Subspecies albicaulis and Subspecies onsimilis

he subspecies are neighboringly sympatric ithout observable introgression in many parts f their ranges; ssp. albicaulis is more montane nd ssp. consimilis more in the valleys. On the nake River plains of southern Idaho, the two re biotically sympatric, and there they ntergrade extensively.

here is considerable variability within each ubspecies. The Idaho phase of ssp. consimilis as been called oreophilus; the predominant hase in California has been called viridulus. he populations in Baja California are morpholoically similar to the Nevada forms of ssp. conimilis even though the California forms are loser geographically.

ap 4. Subspecies consimilis and Subspecies ololeucus

he taxa are sympatric over most of their anges. In the Great Basin, ssp. consimilis refers the lower sites that are more saline, hereas ssp. hololeucus likes the betterrained, less saline sites. The two occaionally are found side by side and show no igns of intergradation. If C. nauseosus were epresented only by ssp. consimilis and ssp. ololeucus, the two would be recognized at the pecies level.

ap 5. Subspecies consimilis and Subspecies raveolens

he subspecies are closely related morphologially. They are largely allopatric, but they ave a greater degree of range overlap than is ound between ssp. albicaulis and ssp. nauseosus map 1). These subspecies (map 5) do intergrade ut to a much smaller degree than ssp. albiaulis and ssp. nauseosus do. Intergradations etween ssp. consimilis and ssp. graveolens are een in southwestern Wyoming, south central Utah, and western New Mexico. They remain distinct in northern Arizona. Populations of ssp. consimilis in the San Luis Valley of Colorado are disjunct from their western counterparts but seemingly do not intergrade with ssp. graveolens.

Map 6. Subspecies graveolens and Subspecies hololeucus

The subspecies are mostly allopatric but share mutual range over a portion of Utah and extreme northwestern Arizona. The subspecies are considered rather widely separated taxonomically. They do not intergrade in their common ranges from central Utah to northwestern Arizona. In eastern Utah and adjacent Colorado, introgression is evident where many plants with the general aspect of ssp. graveolens have woollywhite stems like ssp. hololeucus. The names falcatus and nivecaulis have been applied to specimens with these introgressed characteristics. I include them under ssp. graveolens because their total morphology is closer to that than to ssp. hololeucus.

Map 7. Subspecies graveolens and Subspecies nauseosus

The subspecies are sympatric over approximately half of their respective ranges from western North Dakota to central Colorado. They are frequently biotically sympatric and show little or no intergradation.

Map 8. Subspecies bigelovii, Subspecies leiospermus, and Subspecies mohavensis

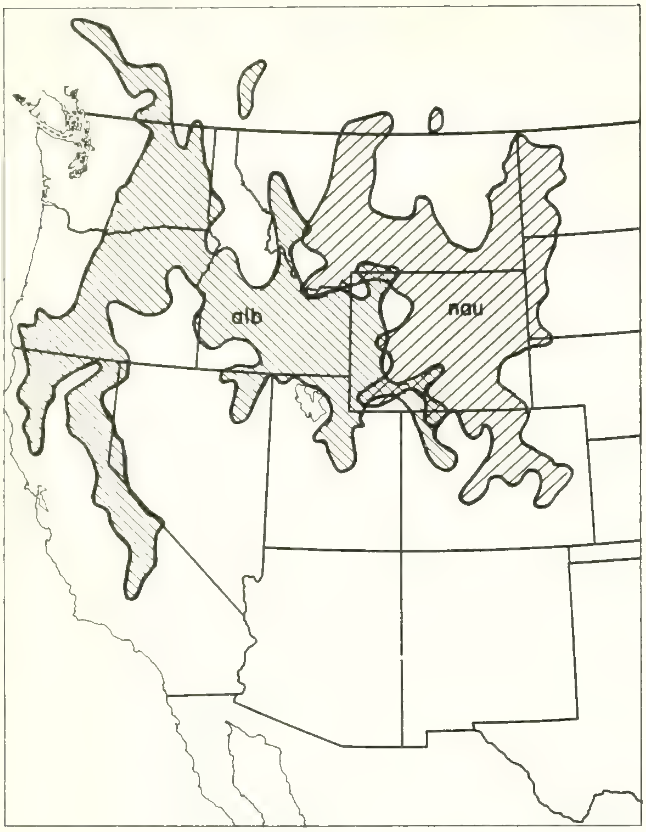
This set of subspecies will serve as final examples for geographical relationships in C. nauseosus although many others could be included. The three have strongly distinguishing morphologies when compared one to another, yet there is limited intergradation in portions of their joint ranges.

Specimens of ssp. bigelovii and ssp. leiospermus are rarely mistaken for one another because they are so distinctive. In extreme southeastern Utah where their ranges overlap, however, specimens that are intermediate between these subspecies are frequently found.

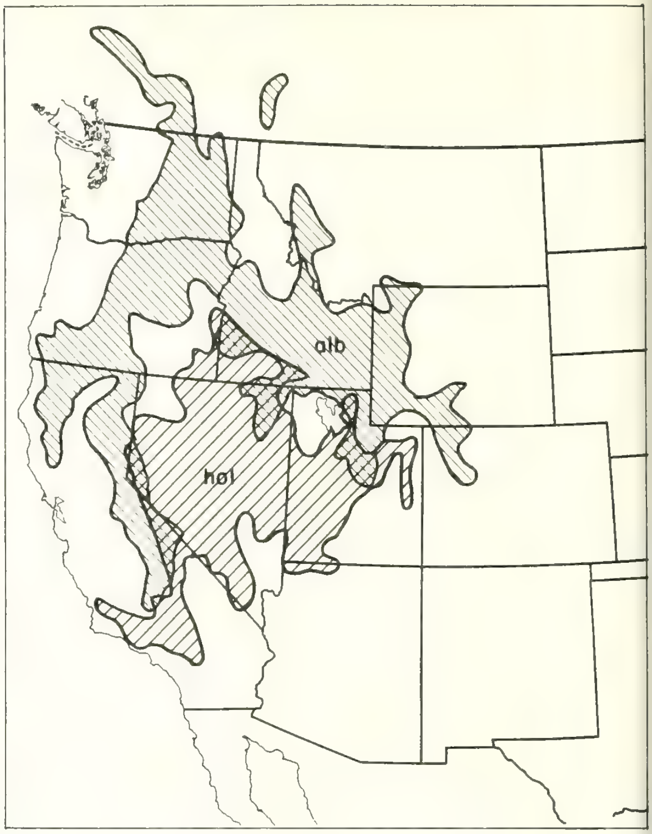
Subspecies leiospermus and ssp. mohavensis maintain their integrity in their range overlap in California, but in the Spring and Pine Valley Mountains of Clark County, Nevada, introgression between the two is evident. Here, some plants that look like ssp. mohavensis have shorter involucres than usual and have glabrous achenes. Also, some plants that look mostly like ssp. leiospermus have slightly longer involucres and very sparse pubescence on their achenes.

DISCUSSION

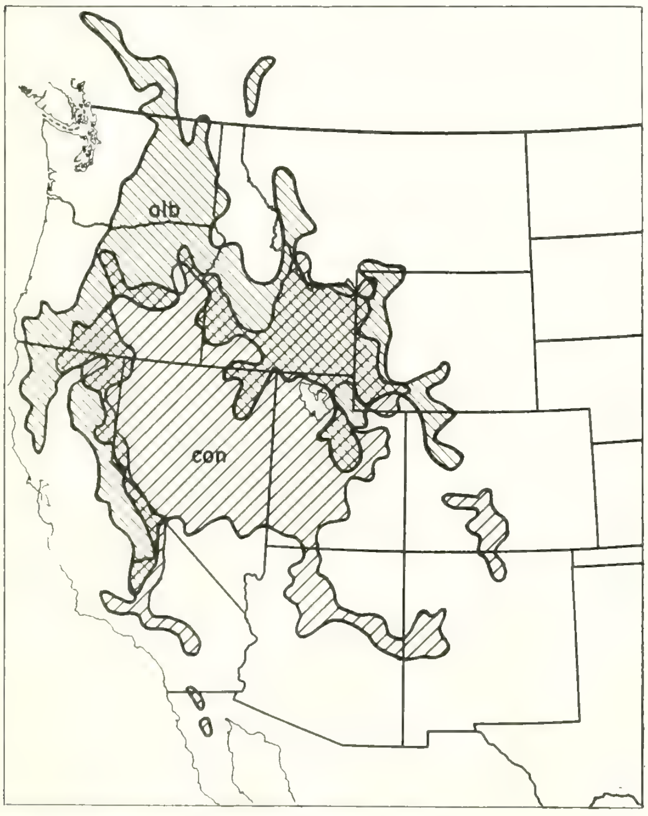
Hall (1919) identified two series within C. nauseosus: the gray forms and the green forms.



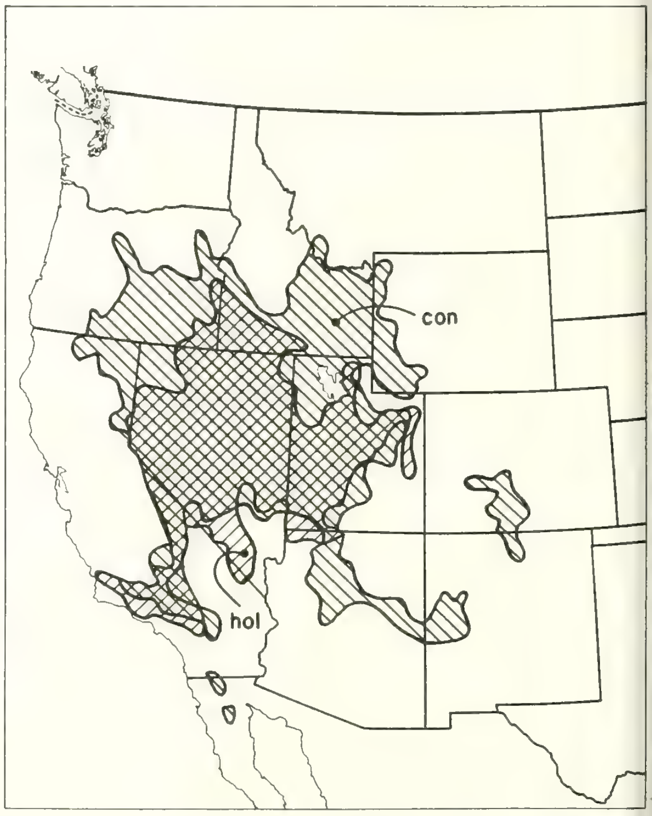
Map 1.--Ranges of ssp. albicaulis (alb) and ssp. nauseosus (nau) in western United States and Canada.



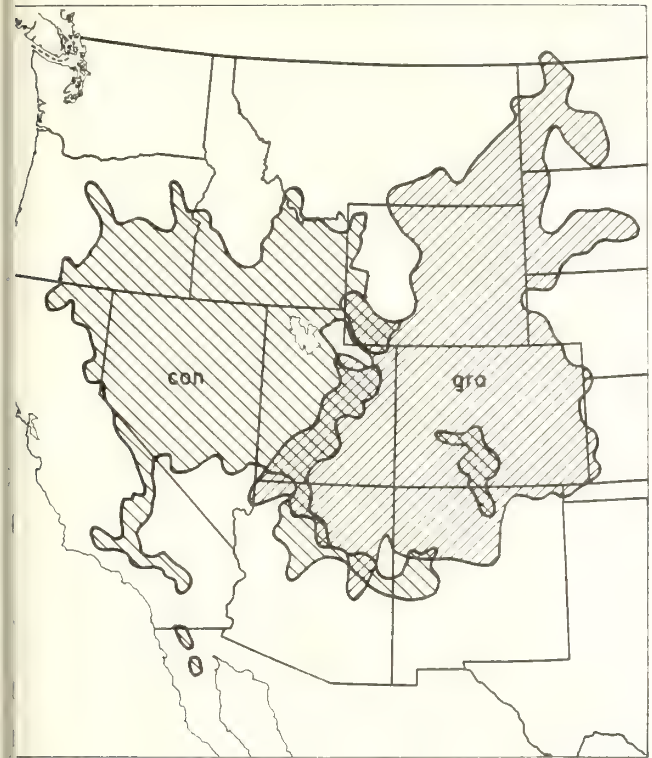
Map 2.--Ranges of ssp. albicaulis (alb) and ssp. hololeucus (hol).



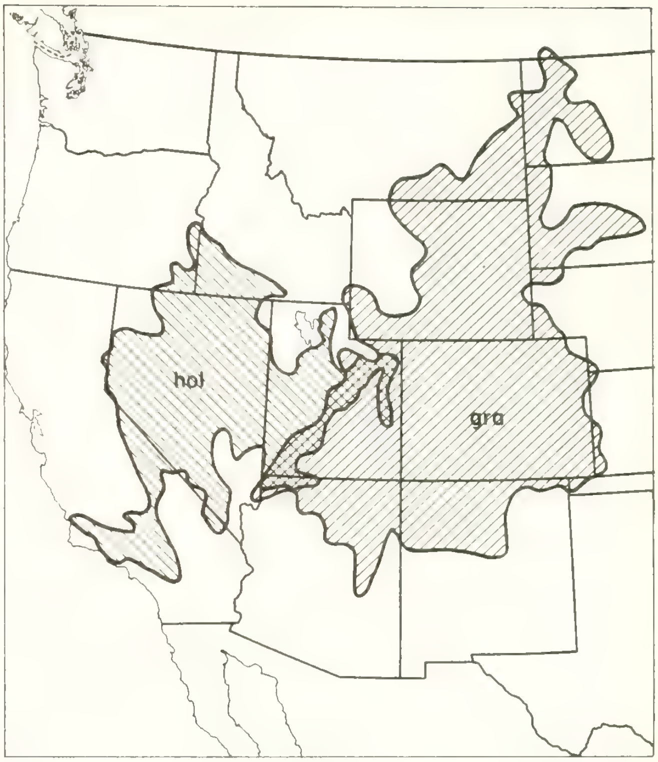
Map 3.--Ranges of ssp. albicaulis (alb) and ssp. consimilis (con).



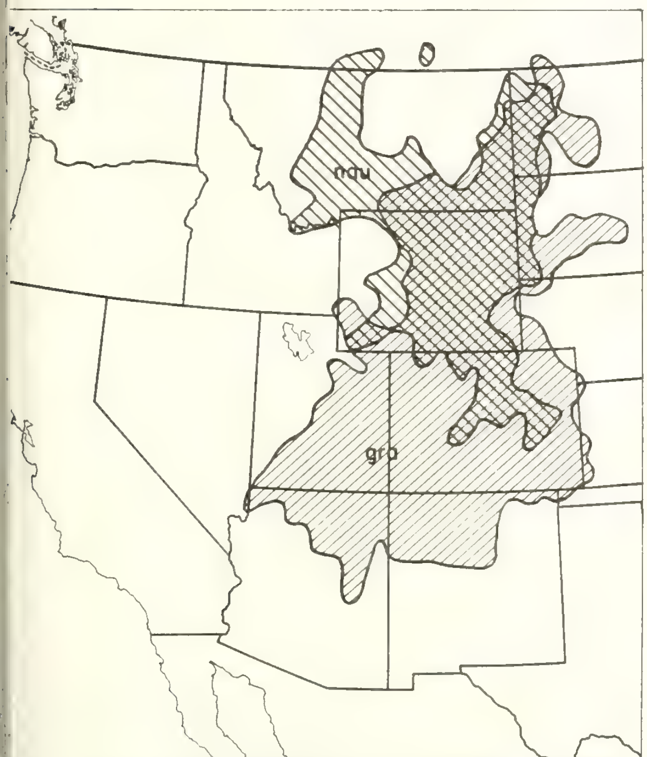
Map 4.--Ranges of ssp. consimilis (con) and ssp. hololeucus (hol).



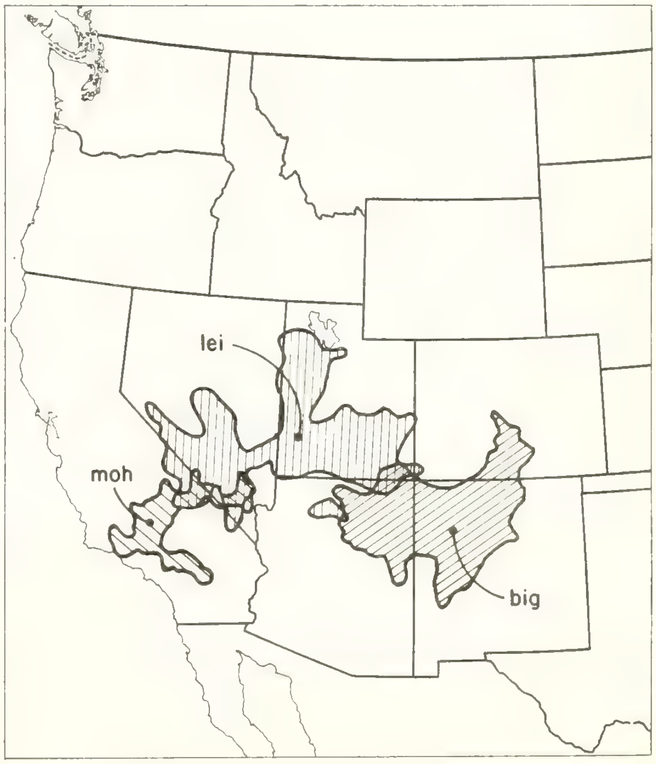
ap 5.--Ranges of ssp. consimilis (con) and ssp. raveolens (gra).



Map 6.--Ranges of ssp. graveolens (gra) and ssp. hololeucus (hol).



ap. 7.--Ranges of ssp. graveolens (gra) and ssp. auseosus (nau).



Map 8.--Ranges of ssp. bigelovii (big), ssp. leiospermus (lei), and ssp. mohavensis (moh).

The gray forms have tomentulose involucres and gray to whitish foliage and stems (and include ssp. albicaulis, bigelovii, hololeucus, and nauseosus as discussed here). The green forms have glabrous involucres and greenish leaves and stems (like ssp. consimilis, graveolens, leiospermus, and mohavensis). Most observations here tend to support the recognition of the two series. Subspecies albicaulis intergrades fairly frequently with ssp. hololeucus and nauseosus (all of the gray group), whereas intergroup associations such as those of ssp. consimilis with hololeucus and ssp. graveolens with nauseosus show very limited or no intergradation. The distinctness of the two color series is weakened with cross-group intergradations such as those of ssp. albicaulis with consimilis, ssp. bigelovii with leiospermus, and ssp. hololeucus with graveolens.

Introgression between subspecies of C. nauseosus is variable relative to distribution patterns of the taxa involved. In some, such as ssp. albicaulis and ssp. nauseosus, the taxa are allopatric (parapatric) and intergrade rather frequently along their contact zone. Other cases show different degrees of sympatry with limited to frequent intergradation. Usually the intergradation does not occur throughout the mutually occupied area but is limited to a portion of the joint range. This phenomenon is most pronounced in the case of ssp. hololeucus and ssp. graveolens (map 6), where exchange occurs only at the eastern range limit of ssp. hololeucus. Apparently some breakdown of internal genetic barriers accompanies the general stressing that must occur in those geographically peripheral populations; the two subspecies do not intergrade in other parts of their mutual range. Finally, there are cases in which taxa can be extensively sympatric but seemingly fail to introgress (maps 4 and 7).

Figure 1 illustrates levels of presumed gene exchange among the major subspecies discussed here. Addition of other subspecies to figure 1 would result in a reticulate maze. For example, ssp. mohavensis hybridizes with ssp. hololeucus (Anderson 1973) and intergrades with ssp. albicaulis and ssp. consimilis to some degree as well as with ssp. leiospermus (map 8). A few specimens from southern California appear to have mixed characteristics of ssp. bernardinus, consimilis, hololeucus, and mohavensis.

Some of the variation in C. nauseosus could be described as an overlapping ring of races: ssp. nauseosus mixes (genetically) with ssp. albicaulis, which mixes with ssp. consimilis, which in turn mixes to some degree with ssp. graveolens. But ssp. graveolens, which occurs with ssp. nauseosus, does not mix with it (fig. 1). Also, ssp. consimilis and ssp. hololeucus do not intergrade, but they have a common associate (ssp. albicaulis) with which each of them does intergrade. I believe ssp. hololeucus is a Great Basin derivative of ssp. albicaulis and ssp. consimilis is a Great Basin derivative of ssp. graveolens. These two Great Basin

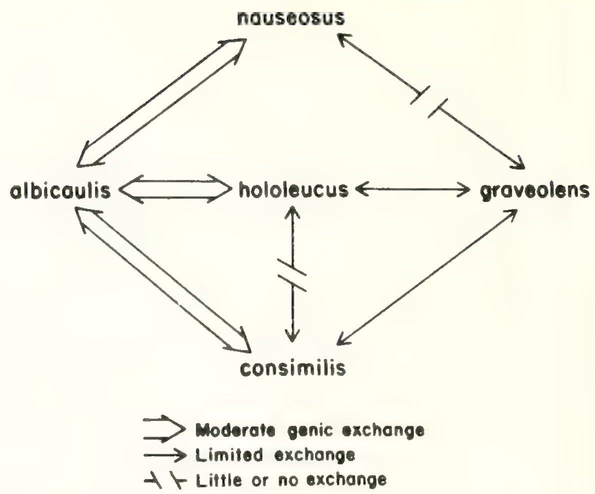


Figure 1.--Relationships among selected subspecies of C. nauseosus (parapatric or sympatric); those not connected by continuous or broken arrows are allopatric and do not intergrade.

subspecies are at a level of divergence that enables them to behave like sympatric species. Most of the subspecies discussed here are at intermediate levels of divergence and reproductive isolation; such populations are often referred to as semispecies (Grant 1981).

It should be remembered that all subspecies of C. nauseosus are relatively well defined and often coexist with little or no gene exchange. Instances of hybridization and intergradation are discussed here to help understand the interrelationships within this species complex and should not be given inordinate emphasis. Continued sympatricity with only limited gene exchange may allow greater development of internal isolating mechanisms and eventual sympatric speciation. Loss of connecting links in the ring of races would lead to speciation as well.

ACKNOWLEDGMENT

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ESTABLISHMENT AND INITIAL RESULTS FROM A SAGEBRUSH (ARTEMISIA TRIDENTATA) MASS SELECTION GARDEN

Gary L. Noller and E. Durant McArthur

ABSTRACT: This study was undertaken to combine characteristics of two promising sagebrush accessions. One accession, Artemisia tridentata ssp. tridentata from Dove Creek, CO, was chosen because it has high nutritive quality and superior growth rate. The second accession, A. t. ssp. vaseyana from Hobble Creek, UT, was selected because of its high palatability and vigorous multi-stemmed growth habit. Seedlings were planted in a mass selection garden at Meeker, CO, in 1981, and evaluated yearly.

INTRODUCTION

The study was initiated as a result of a severe mule deer (Odocoileus hemionus) die-off in Utah in the early 1950's. A. Perry Plummer assembled a team of Forest Service, U.S. Department of Agriculture, and Utah Division of Wildlife Resources people to study ways of improving deer winter range. Sagebrush became an important object of the study because it was used so heavily, was widely distributed, and establishes rapidly from both transplanting and direct seeding.

A cooperative study was initiated in 1981 between the Intermountain Station's Shrub Sciences Laboratory and the Upper Colorado Environmental Plant Center to establish a mass selection garden at the plant materials center in Meeker, CO.

Distribution and Variability

McArthur and others (1979) indicated that big sagebrush is the most widespread and common shrub of Western North America. Beetle (1960) estimated that it covers approximately 226,374 mi^2 (58 655 000 ha) in 11 western States. Across this wide expanse, Plummer and others (1968) observed that "each geographic area has a distinctive type of big sagebrush" and they differ greatly in preference, growth, seed production, and other characteristics. They (Plummer and others 1968) predicted the possibility of developing improved strains or cultivars for use in revegetation projects.

Importance

Big sagebrush is often the dominant forage in the diet of mule deer during winter in the Rocky Mountains and Great Basin (Leach 1956; Kufeld and others 1973; Tueller 1979; Pederson and Welch 1982). Welch (1983) stated that as a winter food big sagebrush ranks among the highest in digestibility, crude protein, phosphorus, and carotene. Plummer (1974) indicated that big sagebrush is one of the best shrubs available for use in revegetation of depleted winter game ranges in the intermountain area. Plummer and others (1968) pointed out that big sagebrush stands are unexcelled in providing ground cover and forage when grazed properly.

Recent research has pointed out differences among accessions of big sagebrush for preference, growth, winter crude protein content, winter in vitro digestibility, and effects on grass cell wall digestion (Welch and McArthur 1979b; Welch and Pederson 1981; Welch and others 1981; McArthur and Welch 1982; Hobbs and others, these proceedings). No one accession contains all of the important characteristics of highest preference, crude protein, in vitro digestibility, growth, and no effect on grass cell wall digestion. This study is an attempt to combine the superior characteristics into one cultivar of big sagebrush to be used to improve mule deer winter range.

MATERIALS AND METHODS

Plant Collections

One hundred accessions of subspecies of Artemisia tridentata were collected by A. Perry Plummer and his colleagues from throughout their range. From these accessions, E. Durant McArthur and Bruce L. Welch selected 21 that showed the most promise and had a range of natural variation for plantings at Gordon Creek, Salt Creek, and Springville--all Utah sites.

From the 21 accessions, McArthur and Welch selected accessions from Hobble Creek, UT, (Artemisia tridentata ssp. vaseyana--commonly called mountain big sagebrush) and Dove Creek, CO, (A. t. ssp. tridentata--commonly called basin big sagebrush) for crossing. These offered the best early opportunity for improvement in growth rate, growth form, and palatability characteristics (Welch and McArthur 1979a).

Paper presented at the Symposium: Biology of Artemisia and Chrysothamnus, Provo, UT, July 9-13, 1984.

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'lant and Site Description

'ove Creek.--The accession from Dove Creek, CO, 'as selected because it has a high crude protein ontent (16.0 percent) and good growth rate Welch and McArthur 1979a). The Dove Creek site s 3.75 miles (6 km) east of Dove Creek, CO. The oil is deep. The elevation is 6,790 ft (2 070 m). 'ove Creek plants are generally single to few temmed and large statured. Leaves are slender or inear and leaders are generally longer than those n the Hobble Creek plants. Dove Creek plants have strongly pungent aromatic odor.

obble Creek.--The accession from Hobble Creek was elected because of its high utilization (84 percent) y mule deer (Welch and McArthur 1979a). The site s located at the western slope of the Wasatch ountains, approximately 1 mile (1.6 km) up obble Creek Canyon (approximately 2 miles from pringville, UT). The elevation is about 4,900 ft 1 470 m). Soils are generally deep, stream-eposited alluvium and shallower rocky hillside aterials. The Hobble Creek plants are generally maller than the Dove Creek plants, with multiple ain stems. Leaves are broadly cuneate and have a amphorlike fragrance.

rossing Procedures

ne first crossing of the Dove Creek and Hobble reek accessions was done in late September 1980. ne procedures were developed by E. Durant McArthur nd involved using the Dove Creek accession as the other plants. They were located at the Snow Field tation at Ephraim, UT. Pollen was taken from plants ocated at the Hobble Creek site. Each pollen sample as a composite of two or three separate bushes. ive different pollen combinations were used. The ollen samples (branches) were introduced into white ollination bags. These bags were put on mother lants just prior to flower opening, so that pollen or pollination was either introduced or produced the perfect flowers on the mother plants.

eed Production and Seedling Selection

'ed produced from the crossing procedure was ollected in November 1980 and germinated in March 981. Seedlings were tagged and numbered and omising plants were selected. Putative hybrids re evaluated by means of a spectrophotometric alysis (McArthur and Welch 1983). The ocedure was to crush a 10-mg leaf and put it in stilled water. The spectrophotometer measured e amount of coumarin and other water-soluble mpounds present. Coumarins are abundant in the bble Creek plants but present in only small antities in Dove Creek plants. The abundance coumarins in the Hobble Creek plants was nsidered an important genetic marker. Seedlings th the highest concentrations of coumarins re kept for planting.

Planting

A mass selection garden was planted on July 15, 1981, at the Meeker plant materials center. A total of 90 plants were put in 6 rows. Spacing between plants and rows was 10 ft (3 m). Holes were dug, water was added, and potted plants were inserted and covered.

Meeker Environmental Conditions

Environmental conditions at the Meeker plant center are characterized by 16.19 inches (41.1 cm) of annual precipitation, 6,500 ft (1 981.2 m) elevation, and a 90-day frost-free growing season. Winter temperatures of -20 to -30 °F (-28.9 to -34.4 °C) are not unusual. The planting is located on a clay loam soil.

Data Collection

The mass selection garden is evaluated at least twice per year. Each of the 90 plants is examined. A wildlife use evaluation is recorded in early spring to quantify wildlife use. Wildlife use is rated as none, very light, light, moderate, or heavy. It should be noted that the plant materials center is fenced with a 6.5 ft (2 m) fence. However, deer and elk (Cervus canadensis) do get inside the fence. A second evaluation is made in midsummer. Values are recorded for survival, vigor and uniformity, height and crown growth, seed production, and number of main stems. Height and crown growth are measured in centimeters and represent the tallest and widest growth of each plant. The abundance of flowers is estimated to determine potential seed production. Vigor and uniformity of the plants is estimated and given a numerical value (1=low and 9=high). The number of main stems was counted in 1983. This was done to determine whether the crossed plants were more like the Dove Creek parent, which generally has one or few main stems, or like the Hobble Creek parent with multiple stems.

We also plan to examine other factors. Seed viability will be determined from seed samples taken in November 1983. Winter protein content will be established from stem and leaf samples taken in March 1984. Essential oil analysis will be done by chromatograph to compare these plants with the parent Hobble Creek and Dove Creek plants. This test may also produce a sort of fingerprint of these crossed plants. In addition, it may help determine if the plants were self pollinated. We also plan to examine palatability of these crossed plants. This will probably be done by allowing deer to use plants inside an exclosure.

RESULTS

Survival

Survival through 1983 has been good. All but one of the 90 plants are still alive.

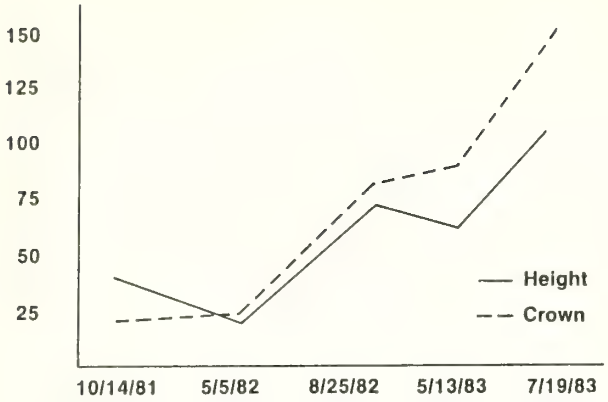

Figure 1.--Plant height and crown width comparisons (cm).

Height and Crown Measurements

The pattern of growth shows that the plants initially had greater height, but with time are now wider than tall (fig. 1). Height decreased from summer to spring readings due to wildlife use and some winter top die-back. Height in 1983 ranged from 29 inches (74 cm) to 50 inches (127 cm) and averaged 40 inches (101.9 cm) (table 1). Crowns in 1983 averaged 55 inches (141.3 cm)

Vigor and Uniformity

The vigor and uniformity rating in 1983 ranged from 5 to 9 and averaged a high 8.2. This indicates the plants were generally vigorous and uniform.

Seed Production

Seed production was first noted in 1982, a little more than a year after planting. In 1982, 66 percent of the plants were flowering. In 1983, all 89 plants were producing seed. The seed production rating averaged 8.4, suggesting high potential seed production (table 1).

Number of Main Stems

The number of main stems in 1983 ranged from 3 to 13 and averaged 6.8 per plant, which points out that the multiple-stem character of Hobble Creek is being expressed.

Table 1.-- Height and crown measurements (cm), vigor and uniformity rating (1=low and 9=high), seed production (1=low and 9=high), and number of main stems in 1983

Characteristic	1983 evaluations (n=49) $\bar{x} \pm$ se	Range
Height	101.9 $\pm$ 1.4	74 - 127
Crown	141.3 $\pm$ 2.2	87 - 188
Vigor/uniformity	8.2 $\pm$ 0.1	5 - 9
Seed production	8.4 $\pm$ 0.2	1 - 9
Number of main stems	6.8 $\pm$ 0.2	3 - 13

Wildlife Use

The crossed sagebrush plants were used by mule deer, white-tailed jack rabbits (Lepus townsendii), and sage grouse (Centrocercus urophasianus). Droppings from these animals were noted in the garden.

Animals use the plants at different times of the year. Mule deer used the plants in late summer and fall, then they migrated out of the area. Sage grouse used the plants at about the same time as mule deer. White-tailed jack rabbits used the plants in winter and early spring before green plants were available. In October 1981 (the year of planting) wildlife made very light use of 44 percent of the 90 plants (table 2). By May 1982 (from fall to next spring) 52 percent of the plants had moderate use and 48 percent had light use. In May 1983, 17 percent of the plants had heavy use, 46 percent moderate, and 37 percent had light wildlife use. In May 1984, 13 percent of the plants had moderate use, 31 percent had light use, and 29 percent had very light wildlife use.

Table 2.--Wildlife use by years

Use level	Percent Use Oct 1981	May 1982	May 1983	May 1984
None	56	0	0	27
Very light	44	0	0	29
Light	0	48	37	31
Moderate	0	52	46	13
Heavy	0	0	17	0

FUTURE DIRECTION OF PROJECT

The other factors mentioned will be examined (seed viability, winter protein content, essential oil analysis, and palatability). Based on continued performance of the crossed plants, 20 to 25 of the best performing plants will be allowe to cross-pollinate. Seed will be collected from the cross and 90 to 100 plants will be selected for additional evaluation. A plant release is anticipated within a period of about 5 years.

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SELECTION OF A CULTIVAR OF *ARTEMISIA LUDOVICIANA* FOR DISTURBED LAND PLANTINGS

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ABSTRACT: The characteristics of *Artemisia ludoviciana* Nutt. are presented. Comparative evaluations of different accessions and subspecies are discussed with emphasis on the characteristics of the accession 'Summit' recently selected for release. Recommendations pertaining to the culture and use of this selection for planting on disturbed lands are made.

INTRODUCTION

Mining activity, roadway construction, and similar disturbances have created harsh infertile sites throughout a wide topographic area of the western United States. Few plants of any one taxa are capable of growing on such a variety of sites, particularly pioneer species suitable for initial planting (Olsen and Nagle 1965; Thornburg 1982; Rumbaugh 1983; Monsen 1984).

Efforts at the Upper Colorado Environmental Plant Center (Meeker Plant Center) and the U.S. Forest Service, Shrub Sciences Laboratory, have been directed toward the development of plant materials suitable for treating seriously disturbed and erosive sites. Emphasis has been on the selection of herbaceous and woody species adaptable to fresh disturbances that will be effective in stabilizing erosion, that can be easily propagated, and will serve as pioneer species or nurse crops capable of moderating disturbances and facilitating the entry of other desirable species.

Selections of Louisiana sage (*Artemisia ludoviciana* Nutt.), also called Louisiana sagewort, sagebrush, and cudweed, have been tested for use as conservation plantings at locations in Idaho and Colorado for nearly 15 years (Monsen 1975). Initial tests demonstrated the plant to be highly useful on disturbed sites; however, variations among ecotypes have been encountered (Shaw and Monsen 1983). In addition, different subspecies and closely related species are recognized (Estes 1969). Subspecific distribution and rigorous taxonomic treatment of the *A. ludoviciana* complex have not been fully completed.

Selections express differences in vegetative stature, growth rates, and rooting habits. The influence of these factors on survival and plant performance has not been documented. In addition, culture requirements essential to establish and propagate plants on wildland disturbances are undefined. Consequently, selections from various plant communities and different sites were assembled in an attempt to develop a genetically superior cultivar suited for wildland uses.

DISTRIBUTION

Artemisia ludoviciana is a widely diverse taxa. Numerous subspecies are described and intergra in areas of overlapping occurrence. It grows naturally over a wide range of soil conditions with populations existing at elevations over 10,000 ft (3 000 m) to less than 3,000 ft (900 m) throughout western North America (Estes 1969).

Four principal subspecies, described by Harrington (1964), occur in Colorado: *A. ludoviciana* ssp. *ludoviciana*, *A. ludoviciana* ssp. *albula*, *A. ludoviciana* ssp. *incompta*, and *A. ludoviciana* ssp. *mexicana*. Plants differ d to the parted or divided condition of the primary leaves and the shape of the panicle. The four subspecies intergrade somewhat, although each occurs in distinct regions. *Artemisia ludoviciana* ssp. *ludoviciana* is more abundant and widespread; *A. ludoviciana* ssp. *incompta* occupies restricted areas at much higher elevations.

Some subspecies reproduce aggressively by spreading rhizomes while others express weak rhizomes. Most produce seed adequately with flowers that can be self or open pollenated. Alpine subspecies are generally decumbent compared to the upright forms found at lower elevations.

POTENTIAL VALUE

As forage, Louisiana sage is not highly value yet it is used by sheep, mule deer, and other game animals and may be seasonally important their diets (Hermann 1966; McCulloch 1973).

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Some attempts have been made to remove the plant from native grasslands to increase production of more desirable species. Louisiana sage usually occurs in scattered amounts and does not dominate extensive areas. Its presence and composition often fluctuate; frequently it is more prevalent following fire or clearing practices that reduce the dominant species. Plant density may slowly diminish as other species recover. Thus, it does not seriously affect the presence or production of other species.

Louisiana sage frequently exists on exposed ridges and sites free of snow accumulation. Under these conditions, the plant receives select use during fall and winter. When frozen, most of the stems and leaves die back to ground level. The dead material apparently does not cure well, as wintering animals normally consume only green tissue. Some forms produce a large rosette of green leaves that remains until late winter.

Although Louisiana sage has not received much attention as a forage plant, it is recognized as a useful conservation species. Farnsworth and Hammond (1968) discussed possible nodulation and nitrogen fixation by this species. Nodulation has been inconsistent, and it has been difficult to confirm any significant degree of nitrogen fixation. In fact, Wullstein and Harker (1982) could not confirm nodulation or nitrogen fixation.

The plant is known to naturally invade and grow vigorously on mine and roadway disturbances. Plants can also be successfully seeded and will spread readily by root proliferation. The extensive root system, a dense coarse root mass 1 to 4 inches (3 to 10 cm) below the soil surface, significantly reduces erosion. The aboveground biomass contributes to reduced erosion, but seldom reflects the extensive subsurface root mass. Plants are not seriously affected by moderate sedimentation or surface slippage, and actually spread with some soil burial. Louisiana sage encourages other species to invade its stabilized space, serving as a very unrestrictive nurse crop.

The potential conservation features of Louisiana sage may be summarized as follows:

1. Different subspecies and ecotypes occur over a wide range of plant communities, extending from semiarid shrublands to subalpine conditions. Diverse taxa provide extensive genetic materials for plant selection and development.

2. Plants develop considerable variability in vegetative and rooting habits suitable to soil stabilization.

3. Plants express excellent establishment characteristics and can spread quickly on harsh disturbances.

4. Established plants serve as an excellent nurse crop that promotes the invasion of other species.

5. Plants are well-suited to infertile soils and appear to improve soil fertility and tilth.

SELECTIONS UNDER STUDY

In the cooperative testing program of the Shrub Sciences Laboratory and the Meeker Plant Center, 22 accessions of Louisiana sage were selected for advanced evaluation. The plant materials originated from native sites in Idaho, Utah, and Colorado (table 1). Plants were assembled for reclamation uses in the mountain West on different site conditions: (1) harsh, cold sites at elevations above 4,000 ft (1 230 m) receiving 14 to 30 inches (35 to 76 cm) precipitation; and (2) dry, harsh sites, receiving below 14 inches (35 cm) precipitation and occurring at elevations below 4,000 ft (1 230 m).

Table 1.--Collection sites of the accessions selected for advanced evaluation studies

Control number	Collection name	Collection site	Elevation
			(ft)
T40955	Blacks Creek	Ada Co., ID	3,100
T40958	Oakley	Cassia Co., ID	4,600
T40971	Hagerman	Twin Falls Co., ID	2,964
T40952	Leslie	Butte Co., ID	5,500
T40957	Hereford Pasture	Elmore Co., ID	3,690
T40953	Lucky Peak	Boise Co., ID	3,200
T40963	Rocky Bar	Elmore Co., ID	6,350
T40966	Bell Creek	Valley Co., ID	3,156
T40962	Cabarton Road	Boise Co., ID	4,700
T40959	Cascade No. 2	Valley Co., ID	4,500
T40964	Bannock Creek	Boise Co., ID	3,021
T4090	Crouch No. 2	Boise Co., ID	3,021
T21457	Franktown	Douglas, CO	5,800
T40968	Deadwood	Boise Co., ID	5,324
T40970	Ola	Gem Co., ID	2,600
T40969	Meridian	Ada Co., ID	2,800
T40967	Smiths Ferry	Valley Co., ID	4,536
T21474	'Summit'	Bear Lake Co., ID	6,299
T40965	Pine View Reservoir	Rich Co., UT	7,000
T40954	Buckhorn Road	Elmore Co., ID	4,000
T40956	Council No. 1	Adams Co., ID	3,300
T40961	Baumgartner	Elmore Co., ID	4,850

Selections were also planted at the Meeker Plant Center under both irrigated and nonirrigated conditions. Study plots were established to evaluate survival, vigor, cold and drought tolerance, spreadability, seed production and harvestability, leaf retention, and biomass production (table 2).

Although field studies have been conducted at various field locations, the principal results and discussion in this paper are for the Meeker Center.

Table 2.--Selected parameters and performance of 22 Louisiana sage accessions transplanted in two projects at the Meeker Plant Center

Accession origin	Control number	Percent 1st year establish.	2nd year spread/cm Irrig.	2nd year spread/cm Dryland	Ground cover Irrig.	Ground cover Dryland	Percent winter leaf retention	Fall leaf greenness	Fall green sprout abundance
Blacks Creek	T40955	75	19	15	[1]4	6	90	9	7
Oakley	T40958	100	32	18	3	8	95	9	4
Hagerman	T40971	100	39	35	4	2	95	5	4
Leslie	T40952	43	35	--	3	5	90	9	3
Hereford	T40957	100	28	30	3	5	90	9	3
Lucky Peak	T40953	81	20	--	5	8	80	7	3
Rocky Bar	T40963	100	17	30	7	7	95	7	8
Bell Creek	T40966	88	36	28	5	4	70	9	1
Cabarton	T40962	93	30	25	4	2	20	9	9
Cascade #2	T40959	93	38	30	2	3	70	9	2
Bannock	T40964	100	58	45	2	3	80	9	6
Crouch #2	T40960	93	30	35	4	5	90	9	9
Franktown	T24175	100	40	15	5	6	90	3	7
Deadwood	T40968	81	26	--	6	8	95	9	9
Ola	T40970	100	35	30	5	4	90	7	7
Meridian	T40969	91	28	--	4	3	20	9	5
Smiths Ferry	T40967	100	40	30	3	3	30	9	3
Georgetown Summit	T21474	100	41	25	3	6	90	2	5
Pine View	T40965	100	50	40	4	2	90	9	3
Buckhorn	T40954	88	30	--	5	7	95	9	3
Council #1	T40956	88	40	32	4	4	30	7	5
Baumgartner	T40961	63	25	--	6	5	90	9	4

[1]Values 1 to 9 with 1 being the best.

STATUS OF SELECTIONS

Field plantings of Louisiana sage selections have been maintained for approximately 15 years at different locations. Plantings located above 5,000 ft (1 540 m), approximately six entries, appear promising for conservation use. Selection T21474 from Georgetown, ID, has performed the best, and pending Varietal Review Committee approval, is scheduled for release as 'Summit.'

'Summit' establishes most rapidly from sprigs or transplants. It also establishes moderately well from direct seeding. Results from trial plantings on mines in northwestern Colorado have been impressive. At Silverton, CO, 'Summit' spread 78 inches (200 cm) in a 5-year period after being planted on unstable and steep slopes. Other selections have also demonstrated rapid spreadability, but 'Summit' has been the most robust. Selections acquired from south-central Idaho growing on granitic soils and as an understory with ponderosa pine (Pinus ponderosa) also exhibit excellent rooting habits. Collections identified as Bannock Creek and Cascade No.2 are examples. 'Summit' has been one of only a few selections able to survive and spread at high elevations on disturbed soils. Most collections succumb when planted at elevations over 9,000 ft (2 769 m). Selections are usually well adapted to the elevation from which collected. 'Summit' exhibits a wide range of adaptation to differences in elevation and soils. 'Summit' also grows well on infertile soil, as evidenced by its performance on heavy metal tailing ponds at the Silverton Mine where coarse, sterile sands are subject to wind and water erosion, frost during any month, and an annual precipitation of 18 to 22 inches (46 to 56 cm). Although other selections initially survive when planted at elevations above 5,000 ft (1 540 m), few persist for more than 3 to 5 years Consequently, spreadability and persistence of 'Summit' have accounted for its acceptance. 'Summit' also grows and spreads well on road disturbances when immediate stability is desired.

Grasses may begin to invade plantings of all selections including 'Summit' within 2 to 5 years Tree and shrub entry normally proceeds more slowl As these plants increase, the Louisiana sage decreases. Some invading plants increase dramatically, but recede quickly. Louisiana sage re-emerges to occupy the exposed openings. Seedlings of invading species are observed to establish amid the clumps of Louisiana sage. This response encourages the use of Louisiana sage as a nurse crop to speed up and direct positive succession on poor sites. Studies have not demonstrated that any single selection of Louisiana sage performs better than another as a nurse crop. The aggressive growth habit of 'Summit' has not delayed the invasion of other plants nor appeared to favor certain species.

Since 1982, 'Summit' has been compared with many other excellent-performing selections of Louisiana sage in irrigated and dryland gardens at the Meeker Plant Center. Under agronomic conditions, 'Summit' initiates rhizomes and spreads as rapidly as any comparable type. It has been rated highly for its soil protection

characteristics. In can grow on clays as well as sterile sands. It initiates growth early and is noted for retaining green leaves into the fall (table 2).

Other top-performing lines warranting further comparisons are Pine View, Bannock, Smiths Ferry, Meridian, Council #1, and Hagerman. Hagerman may be best for drier climates at lower elevations. It shows excellent vigor, good early growth, and moderate spread. Pine View has been comparable to 'Summit,' exceeding 'Summit' in vigor and biomass production in garden trials. In the garden trials there are differences in growth habits among accessions and the ease with which other plants invade into the plots. 'Summit' spreads well and is invaded easily.

Very few accessions have illustrated poor winter tolerance. Some, like the Franktown accession, start growing quite slowly in the spring but finish the growing season comparable in biomass and seed production to the top performers. Bannock is a good grower, but lodges early in the fall. Smiths Ferry and Pine View produce an abundance of green sprouts in the fall. Some of the mediocre performers produce an abundance of fall sprouts. Bell Creek is the greatest producer of sprouts in the fall, but has less than the average number of sprouts by spring. Pine View, 'Summit', and Hagerman all do a good job of retaining leaves well into fall, while accessions such as Council #1 lose 70 percent of their leaves by early fall.

SEED PRODUCTION

Field culture of Louisiana sage seed is important for its use in wildland plantings. Selections that can be grown under varied conditions will reduce planting costs and enable expansion of rearing to farms located in different geographical areas.

Seed production studies at the Meeker Plant Center revealed that considerable variability in seed production exists among selections (table 3). A number of selections produce greater amounts of seed than the 'Summit.'

Differences in seed germination have been recorded among accessions when grown at the Meeker location (table 3). Factors that affect seed production and viability are not fully understood. However, inherent differences among accessions and culture treatments, including storage, affect seed quality.

The Meeker Plant Center production fields of 'Summit' were sprigged to establish the plantings, using about 1,100 sprigs (4 bushels) to the acre (0.35 m^3/ha) irrigated. The rows were set on 6-ft (1.8-m) centers and sprigs were set 12 inches (30 cm) apart in the row. Seed fields established from sprigs produced seed by the end of the second growing season. Seed culture techniques have a marked influence upon yields.

'Summit' seed yields have reached 84 pounds cleaned seed per acre (94 kg/ha); however, yields have been reduced by excessive shatter created by loose seed heads damaged by seed head insects identified as immature Psyllids, order of Homoptera, family Psyllidae. The timing of harvest is critical because the seed heads quickly mature and shatter.

Standard combines and cleaning equipment can be used to harvest and process the seed. The seed retains high levels of dormancy and often has a germination value of 30 to 48 percent with a purity over 90 percent. Dormancies have ranged from 30 to 40 percent.

Seed production enhancement studies on 'Summit' have been initiated at the Meeker Plant Center (table 4). These studies evaluate seed production responses to fertilizer levels, fall and spring tillage, chemical and implement stripping, and use of systemic insecticides.

Variability within each plot and between similar treatments indicates soil variability may override treatment response differences. Fall-fertilized plot J produced the most biomass, while its counterpart, plot A, produced less than the 8,548-pound average for all plots, but more than the control. Seed yield data are not available at this time, however, seed yields respond similarly to herbage production. Fall-applied fertilizer treatments were consistently the most productive.

SEEDING RECOMMENDATIONS

Although plantings of Louisiana sage can be accomplished by transplanting, direct seeding is the most practical approach for large projects. Seeds are very small for all selections tested. No single selection appears to establish better by direct seeding. All selections grow rapidly, and thus compete well in mixtures with other herbs. Fall seedings have been most successful. The tiny seed (approximately 3,000,000/lb [6.6 million/kg]) should be seeded at very shallow depths at a rate of one-quarter pound or less per acre (280 g/ha). Seed size and depth of planting create problems when using a standard drilling operation. When seeded in mixtures with seed of other species, Louisiana sage seeds separate rapidly, falling to the bottom of the drill box.

Stands have been successfully established by broadcasting the seed followed with a light harrowing. Drill seeding can be improved by using a commercial sticker that attaches the seed to perlite, which then can be mixed with a bulky seed mix and seeded through the trashy seed box on a drill. This second system allows the seed to be metered and dropped on the surface immediately in front of the press wheels.

Pelletizing the seed helps resolve the seed size problem. In a greenhouse trial in cooperation with Germain's, Inc., 'Summit' seed was coated

Table 3.--Variability of seed production in Louisiana sage accessions in a uniform garden

Accession number	Seed abundance	Seed stock height(cm)	Uniformity	Standability	Harvestability	Uniform maturity	Pounds per/acre	Percent germination
T40959	[2]2.5	93	[2]2.0	[2]3.0	[2]2.5	[2]1.5		
T40962	3.5	58	2	6	4	2.5	320	
T40953	1.5	86	3	1	1	3	1142	[1]77.5
T40971	2	101	2	2	2	2.5	955	51
T40955	3	90	4	4	3.5	3.5		
T40958	2	82	2.5	2	2	3	365	
T40968	3.5	110	1.5	1	2.5	3	152	
T40964	2	108	2	4	3	2.5	296	
T40952	2.5	100	2	4	2.5	2	1032	36.5
T40960	3	88	2	3.5	3	2	572	32.7
T40957	2	104	2.5	4	2.5	3	624	46.5
T40963	4	88	1.5	2.5	3	3		
T21474	2	82	2.5	3.5	3	3		
T40970	3	86	1	1	2	2.5	122	
T40969	1	98	1	1	1	1	441	
T40966	1	85	2	3.5	2.5	1.5	411	
T40956	1.5	109	2	2.5	2	2	1970	37
T40967	3	94	2.5	3.5	2.5	2	638	25.2
T40954	3	52	2	1	2	2	660	21
T21475	2.5	78	3	2	2	2	15	
T40961	3	91	3	3.5	2	2.5		
T40965	2	88	2	1.5	2	2		

[1]Data only for those tested.
[2]Values 1 to 10 with 1 being best.

Table 4.--Initial results of seed enhancement treatments on a 'Summit' Louisiana sage production field

Plot	Treatment	Dry weight per/acre	Uniformity	Seed stalk abundance	Height by percent of plot
A	Fertilize 30-46-0	7295	[1]5	6	15% - 73 cm, 85% - 34 cm
B	Control	6780	5	5	20% - 65 cm, 80% - 40 cm
C	Fertilize 34-0-0	10679	5	5	20% - 70 cm, 80% - 30 cm
D	Spring chisel	5901	6	5	10% - 66 cm, 90% - 30 cm
E	Fertilize 90-30-0	10326	5	4	20% - 67 cm, 80% - 34 cm
F(a)	Spring strip	8601	4	5	70% - 66 cm, 30% - 46 cm
F(b)	Spring Roundup	6214	4	6	80% - 40 cm, 20% - 18 cm
G	Insecticide	9350	3	5	50% - 60 cm, 50% - 32 cm
H	Chisel/24-30-0-21	8308	4	5	40% - 70 cm, 60% - 40 cm
I	Fall chisel	9580	4	5	50% - 68 cm, 50% - 40 cm
J	Fertilize 30-46-0 (Fall)	11003	2	2	30% - 89 cm, 70% - 57 cm
Average		8548			

[1]Values 10 to 10 with 1 being best.

at two different ratio levels, one at 18 to 1 and the other at 26 to 1. By random sample count, the 18 to 1 ratio reduced the number of units per pound from 3,000,000 to 240,000 and the 26 to 1 to 129,000 (530,000 to 285,000/kg). Germination was not reduced by the 18 to 1 coating level; however, the 26 to 1 coating reduced germination by 50 percent.

CONCLUSIONS

Louisiana sage T21474 was selected for release as 'Summit' primarily based on its performance on extremely harsh sites, persistence, ability to reduce erosion rapidly, wide area of adaptation, leaf retention, quality of all green foliage, and apparent outstanding ability to serve as a nurse crop[1]. Studies are currently being conducted to determine methods for seed production and processing. Plantings have demonstrated that Louisiana sage can be used to colonize harsh sites and improve site conditions for other species.

[1]More exhaustive data documenting the performance and release of 'Summit' Louisiana sage is available from the Meeker Plant Center.

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Section 3. Revegetation and Plant Control

HERBICIDE USE IN ARTEMISIA AND CHRYSOTHAMNUS COMMUNITIES: REDUCING DAMAGE TO NONTARGET SPECIES

Steven G. Whisenant

ABSTRACT: In 1983, a series of experiments was conducted in Utah to compare selectivity and effectiveness of clopyralid, 2,4-D, dicamba, and picloram. Big sagebrush, threadlead rubber rabbitbrush, and stickyleaf low rabbitbrush can be controlled using any of these herbicides. Preliminary results suggest that clopyralid will control rabbitbrush without damaging members of the Rosaceae family.

INTRODUCTION

Sagebrush Ecosystem

Big sagebrush (Artemisia tridentata) occupies a substantial portion of the western United States: over much of Utah, Nevada, southern Idaho, eastern Oregon, western Montana, Wyoming, and Colorado, as well as smaller areas in Washington, California, Arizona, and New Mexico (Tisdale and others 1969). Estimates of the size of the sagebrush ecosystem range from 94 million acres (38 million ha) (USDA Forest Service 1972) to 269 million acres (109 million ha) (Beetle 1960). Either estimate indicates that the sagebrush ecosystem is one of the largest range ecosystems in the United States.

Many important shrubs and herbaceous species are associated with sagebrush (Blaisdell and others 1982). This species diversity is an important aspect of the sagebrush ecosystem. Partially because of this diversity the sagebrush ecosystem is inhabited by a wide variety of mammals and birds. Antelope, mule deer, elk, sage grouse, mourning doves, and chukar partridges are the most important game species (Garrison and others 1977).

The size, accessibility, and productive potential of the sagebrush ecosystem make it an important resource for production of livestock and wildlife, watershed values, and a variety of recreational activities. Unfortunately, much of the sagebrush ecosystem has been degraded by abusive grazing. As a result, the sagebrush ecosystem is still far below its potential production of livestock forage and wildlife habitat (USDA Forest Service 1972).

A primary problem of the sagebrush ecosystem is the increase in density and size of sagebrush and other low-value shrubs, accompanied by the reduction in perennial grasses and forbs. Sagebrush stands frequently become dense enough to reduce forage production and inhibit livestock movement (Blaisdell and others 1982). Because of its long life and ability to compete with perennial herbs for soil-water and nutrients, sagebrush in dense stands is a serious obstacle to range improvement through grazing management or seeding of desirable plant species (Blaisdell 1953).

Depending on its density, size, and inherent palatability, big sagebrush may either be a valuable component of the community or a problem (Blaisdell and others 1982). Big sagebrush in proper mixtures with other shrubs, forbs, and grasses is critical for sage grouse (Klebenow 1969) and antelope (Yoakum 1980) habitat. It is a superior winter forage for mule deer because of its high crude protein content and coefficient of digestion (Welch and McArthur 1979a,b). However, despite its importance, it can become too plentiful at the expense of other desirable plants. Despite the prominence of sagebrush in their diet, antelope do best where the shrub cover is moderate and low in stature (Urness 1979; Yoakum 1980). Sage grouse do not nest in, nor do broods occupy areas of tall, dense sagebrush with little understory (Klebenow 1969). Domestic livestock, particularly sheep, use the more palatable forms of sagebrush but do much better with a greater diversity of food items.

Rabbitbrush

The rabbitbrushes (Chrysothamnus spp.) occupy a wide variety of habitats in western North America. They occur on open plains, valleys, foothills, and mountains from sea level to 10,900 feet (3 300 m) in elevation (Hitchcock and others 1969). At least eight species occur in the intermountain area. Most herbicide control efforts have been directed at two of these species: rubber rabbitbrush (Chrysothamnus nauseosus) and low (green, Douglas) rabbitbrush (Chrysothamnus viscidiflorus).

Rubber rabbitbrush ranges from Saskatchewan and British Columbia south to eastern California,

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Baja, and western Texas. It is common on plains, valleys, and foothills. It grows best in openings within the sagebrush, pinyon-juniper (*Pinus edulis-Juniperus*), and ponderosa pine (*Pinus ponderosa*) zones on sandy, gravelly, or clayey alkaline soils from 500 to 9,000 feet (150 to 2 750 m) (McArthur and others 1979). Rubber rabbitbrush vigorously invades disturbed sites such as roadcuts and overgrazed rangelands. Destroying big sagebrush with fire or heavy grazing may cause rubber rabbbitbrush to increase and become the dominant vegetation (Evans and others 1973). At least four subspecies of rubber rabbitbrush are found in the intermountain area. Some of these subspecies vary greatly in their value as browse (McArthur and others 1979) while others are sympatric and hybridize.

Low rabbitbrush occurs on dry, open areas and is one of the most widely distributed shrubs on western North American rangelands. It is found between 2,600 and 11,000 feet (790 and 3 300 m) from British Columbia and North Dakota south to New Mexico, Arizona, and California (McArthur and others 1979). Low rabbitbrush is usually associated with sagebrush, snakeweed (*Gutierrezia*), and other species of rabbitbrush. This species may rapidly increase on overgrazed or otherwise disturbed sites. Following a fire, low rabbitbrush increases by basal sprouts and seedling establishment. Low rabbitbrush continues to dominate for at least 15 years (Young and Evans 1974). Some subspecies adapt well to higher elevations while others do best in lower desert and foothill habitats (Plummer 1977).

Vegetation Management

Restoration of desirable vegetation seldom is obtained solely through improved grazing management or even by eliminating domestic livestock. Improvement of degraded sagebrush communities in a reasonable length of time usually requires practices such as prescribed burning, herbicides, or mechanical control. Biological measures using insects, diseases, or mammals are also possibilities.

Fire is often successfully used for sagebrush management. However, under some circumstances fire may have undesirable results. Many sagebrush communities are difficult to burn except under hazardous burning conditions (Evans and others 1979). If few herbaceous perennial plants are present, the stand becomes more difficult to burn and the chances of increasing undesirable shrubs, such as rabbitbrush or annual grasses, are greatly increased. Some perennial grasses are susceptible to damage or are killed by burning at certain times in the growing season (Wright and Klemmedson 1965).

The use of large anchor chains to uproot sagebrush and rangeland plows to plow sagebrush communities has been extensive. However, the lack of selectivity and high energy costs of many mechanical methods have greatly reduced their use. Chaining may stimulate species, such as rabbitbrush, which resprout from basal buds following disturbance.

Biological methods of sagebrush control using insects and diseases are still in the research phases. Biological control may require the introduction of exotic insects or pathogens, a procedure which requires extreme caution. However, present knowledge indicates some degree of sagebrush control may be possible using sheep (Frischknecht 1979) or goats (Urness and Jensen 1983) as control agents.

Suitability of a particular method depends upon such factors as density, height, and age of the sagebrush stand, associated shrubs, amount and kind of herbaceous vegetation, topography, soils erosion potential, available equipment, size of area to be treated, planned use of area, economics, and even personal preference. In many situations herbicides have been the chosen method.

Herbicides

Following World War II, the discovery of 2,4-D ((2,4-dichlorophenoxy)acetic acid) as a plant growth regulator led to the development of herbicides for the control of sagebrush (Bovey 1971). This was the first truly selective herbicide used on rangelands since monocots such as grasses were undamaged by 2,4-D. After a few years of widespread use, it became apparent that root-sprouting subdominant shrubs in sagebrush communities were relatively difficult to kill with 2,4-D compared to big sagebrush (Young and others 1981). Low rabbitbrush control required careful timing of 2,4-D for success. Phenological development was later integrated with soil-water content to predict the best 2,4-D application date for low rabbitbrush control (Hyder and others 1958).

Because of the often undesirable effects of 2,4-D on nontarget species, vegetation composition should be carefully considered before treatment. Perennial grasses are seldom damaged and usually increase as a result of reduced competition from sagebrush. Unfortunately, many desirable perennial forbs and shrubs are severely damaged by 2,4-D. This damage should be evaluated relative to the anticipated benefits of the herbicide treatment.

Among the important forbs moderately or severely damaged by 2,4-D are arrowleaf balsamroot (*Balsamorhiza sagittata*), milkvetch (*Astragalus stenophyllus*), one flower sunflower (*Helianthella uniflora*), several lupines (*Lupinus* spp.), and bluebell (*Mertensia oblongifolia*) (Blaisdell and others 1982). The loss of forbs has been considered a major problem with the use of herbicides on sage grouse range (Autenrieth 1981).

Carpenter (1974) demonstrated that, under certain conditions, sagebrush can be controlled with 2,4-D without forb damage. Applications of 2,4-D on April 4 (with some snow cover) killed 26

percent of the sagebrush with no forb mortality. Twenty-six percent mortality may be considered a failure for many purposes, but was ideal for thinning sagebrush on sage grouse range. Application of 2,4-D on April 17 killed 63 percent of the sagebrush and 17 percent of the forbs. Later applications were more damaging to forbs. Autenrieth (1981) suggested winter applications of a contact herbicide, such as glyphosate (N-(phosphonomethyl) glycine) be tested, to kill sagebrush without forb damage.

Damage to other shrubs, though often temporary, may be severe. Aboveground portions of snowbrush (Ceanothus velutinus), aspen (Populus tremuloides), chokecherry (Prunus virginiana), and snowberry (Symphoricarpos oreophilus) are easily damaged by 2,4-D. These species resprout vigorously, but production of foliage and seed is greatly reduced for several years (Blaisdell and others 1982). Serviceberry (Amelanchier alnifolia) is severely damaged by 2,4-D and may not resprout. Pechanec and others (1965) found serviceberry to be among the shrubs most susceptible to 2,4-D damage. Resprouting of serviceberry following 2,4-D damage was reported by Mueggler (1966) and Ferguson (1983). Gratkowski (1978) reported that serviceberry sprayed with 2,4-D had not recovered its original vigor after 19 years.

Bitterbrush (Purshia tridentata), an important forage species for both livestock and big game, is somewhat resistant to spraying provided the plants are mature. Young bitterbrush plants are very susceptible to 2,4-D (Hyder and Sneva 1962). Phenological selectivity was successfully demonstrated (Hyder and Sneva 1962) with the use of 2,4-D to control big sagebrush without killing bitterbrush. Big sagebrush plants start growth earlier in the spring than bitterbrush. When 2,4-D applications are carefully keyed to these phenological differences, selectivity can be obtained. Application of 2,4-D between the time of bitterbrush leaf appearance and early fruit development resulted in progressively greater damage. Spraying 2,4-D at any time killed virtually all leaf tissue and current growth of bitterbrush; however, spraying at the time of leaf origin and before the appearance of distinct stem elongation or flowers caused only a small amount of dead tissue on large plants (Hyder and Sneva 1962). Subsequently, dormant buds initiated new growth, and by autumn only slight evidence of injury remained. Hyder and Sneva (1962) summarized by stating that the proper timing for spraying 2,4-D on mixed stands of big sagebrush and bitterbrush on dry sites is indicated by the appearance of (1) new leaves on big sagebrush and bitterbrush and (2) heads on Sandberg bluegrass (Poa sandbergii). Spraying may continue until bitterbrush is in flower.

Chemical properties of herbicides may also provide a means of selectivity. Soil-active herbicides with low water solubility may be used to control shallow-rooted species without damaging deeper-rooted species. This form of selectivity is routinely used in agronomic situations. In rangelands it forms the basis of atrazine (2-chloro-4-(ethylamino)-6-(isopropylamino)-s-triazine) selectivity between cheatgrass (Bromus tectorum) and the deeper rooted perennial wheatgrasses (Agropyron spp.) This may also be the basis for tebuthiuron's (N-[5-(1,1 dimethylethyl)-1,3,4-thiadiazol-2-yl]-N,N'-dimethylurea) selectivity between sagebrush and bitterbrush. Pelleted formulations of tebuthiuron have been used effectively for big sagebrush (Artemisia tridentata) control (Whitson and Alley 1984). Bitterbrush and serviceberry are relatively unharmed by tebuthiuron rates commonly used for sagebrush control (0.4 to 0.7 lb/ac, 0.44 to 0.75 kg/ha). Rabbitbrush is unaffected by rates of up to 2.0 lb/ac (2.20 kg/ha) tebuthiuron. Increasing precipitation and decreasing amounts of clay and soil organic matter, will move these herbicides deeper into the soil profile, thus reducing selectivity.

Selectivity also may be achieved by avoiding or minimizing contact between the herbicide and desirable plants. This type of selectivity is called placement selectivity and may be just as effective as true selectivity (Anderson 1983), but involves no plant-herbicide interaction. This is usually obtained with individual plant treatments involving only the target species. Individual plant treatments are usually labor-intensive but may be economically feasible under certain situations (Ueckert and Whisenant 1982). Pelleted formulations are well suited to individual plant treatments. Picloram (4-amino-3,5,6-trichloropicolinic acid) pellets control both rabbitbrush and sagebrush and tebuthiuron pellets work well on sagebrush.

Clopyralid (3,6 dichloropicolinic acid) is a new selective hormone-like herbicide somewhat similar to the phenoxy herbicides and picloram in activity. It is highly effective against members of the Polygonaceae, Compositae, and Leguminosae families (Herbicide Handbook Committee 1983). In 1983, a series of experiments designed to compare the selective control potential of clopyralid with 2,4-D, dicamba, and picloram were initiated.

MATERIALS AND METHODS

Herbicides were applied with a CO_2-powered backpack sprayer to plots in Wasatch and Garfield Counties, UT on June 18 and July 20, 1983, respectively. Herbicides were applied at a rate of 15 gal/acre (140 L/ha) in water containing 0.5 percent (v/v) surfactant. Treatments were applied to 10 by 100 ft (3 by 30-m) plots replicated three times in randomized complete block designs.

The Wasatch County study area contained mountain big sagebrush (Artemisia tridentata ssp. vaseyana), bitterbrush, and serviceberry. Clopyralid (monoethanol amine salt of 3,6 dichloropicolinic acid) was applied at the rate of 0.25, 0.50, 1.00, and 2.00 lb/acre (0.28, 0.55, 1.12, and 2.24 kg/ha). One treatment of

2.00 lb/acre (2.2 kg/ha) 2,4-D (propylene glycol butyl ether ester of 2,4-D) was applied. Dicamba (3,6-dichloro-o-anisic acid) and picloram (4-amino-3,5,6-trichloropicolinic acid) are not often used for sagebrush control and generally cause more damage to bitterbrush and serviceberry than 2,4-D. For these reasons, neither dicamba nor picloram were used at this study area. Phenology at the time of spraying was as follows: sagebrush, full leaf expansion and 2 inches (10 cm) of new stem growth; bitterbrush, full flower and leaf expansion; and serviceberry, 2 inches (5 cm) of new stem growth. Temperature was 70°F (21°C) and relative humidity was 43 percent during spraying.

The Garfield County study area contained threadleaf rubber rabbitbrush (Chrysothamnus nauseosus ssp. consimilis), stickyleaf low rabbitbrush (Chrysothamnus viscidiflorus ssp. viscidiflorus), and mountain big sagebrush. Treatments consisted of clopyralid at 0.50, 1.00, and 2.00 lb/acre (0.55, 1.12, and 2.24 kg/ha; 2,4-D at 2.2 kg/ha); dicamba (as the dimethylamine salt) at 3.00 and 4.00 lb/acre (3.30 and 4.40 kg/ha); and picloram (as the potassium salt) at 0.25, 0.50, and 0.75 lb/acre (0.28, 0.55, and 0.83 kg/ha). Phenology at the time of spraying was: sagebrush, flowers unopened; threadleaf rubber rabbitbrush, 4-5 inches (10-12 cm) of new stem growth; and stickyleaf low rabbitbrush, 2 inches (5 cm) of new stem growth. Temperature, during spraying was 72°F (22°C) and relative humidity was 65 percent.

In August 1984, the percent foliar reduction was estimated for each species and plot at both locations. Percentage reduction was subjected to arcsine transformation prior to conducting analyses of variance. Mean separations were made at the 5 percent level of significance using Duncan's multiple range test.

RESULTS

Mountain big sagebrush response.--Canopy reductions of at least 90 percent followed clopyralid applications of 1.00 or 2.00 lb/acre (1.1 or 2.2 kg/ha) at both the Garfield County (table 1) and Wasatch County (table 2) locations. At the Wasatch County study area 2.00 lb/acre (2.2 kg/ha) of 2,4-D reduced foliar canopies by 95 percent (table 2). However, at the Garfield County study area 2.00 and 4.00 lb/acre (2.2 and 4.4 kg/ha) of 2,4-D reduced mountain big sagebrush canopies by 40 and 90 percent, respectively (table 1). Canopy reductions of 100 percent resulted from applications of either 3.00 or 4.00 lb/acre (3.3 or 4.4 kg/ha) of dicamba (table 1). At the Garfield County study area picloram applications of 0.25, 0.50, and 0.75 lb/acre (0.28, 0.55, and 0.83 kg/ha) resulted in reductions in mountain big sagebrush canopy of 20, 80, and 100 percent, respectively (table 1).

Threadleaf rubber rabbitbrush response.--Canopy reductions of 75, 100, and 100 percent followed clopyralid applications of 0.50, 1.00, and 2.00 lb/acre (0.55, 1.10, and 2.20 kg/ha) respectively (table 1). Applications of 2.00 and 4.00 lb/acre (2.2 and 4.4 kg/ha) 2,4-D resulted in 40 and 90 percent reductions, respectively in threadleaf rubber rabbitbrush canopy. Both the 3.00 and 4.00 lb/acre (3.3 and 4.4 kg/ha) rates of

Table 1.--Percentage canopy reduction on August 24, 1984, of threadleaf rubber rabbitbrush, stickyleaf low rabbitbrush and mountain big sagebrush following herbicide applications on July 20, 1983, in Garfield County, UT

Treatment		Canopy reduction		
Herbicide	Rate	Mountain big sagebrush	Threadleaf rubber rabbitbrush	Stickyleaf low rabbitbrush
	Kg/ha	Percent		
2,4-D	2.20	40 c	40 c	35 d
2,4-D	4.40	90 ab	90 ab	90 ab
Dicamba	3.30	100 a	100 a	92 a
Dicamba	4.40	100 a	100 a	95 a
Picloram	.28	20 cd	80 b	75 bc
Picloram	.55	80 b	100 a	85 ab
Picloram	.83	100 a	100 a	100 a
Clopyralid	.55	50 c	75 b	55 c
Clopyralid	1.10	90 ab	100 a	93 a
Clopyralid	2.20	100 a	100 a	100 a
Untreated		10 d	5 d	8 e

[1] Means within a column followed by the same letter are not significantly different ($P \leq 0.05$) according to Duncan's multiple range test.

Table 2.--Percentage canopy reduction on August 23, 1984, of mountain big sagebrush, bitterbrush, and serviceberry following herbicide applications on June 18, 1983, in Wasatch County, UT

Treatment		Canopy reduction		
Herbicide	Rate	Mountain big sagebrush	Bitterbrush	Serviceberry
	Kg/ha	Percent		
2,4-D	2.20	95 a	90 a	100 a
Clopyralid	.28	10 c	10 b	10 b
Clopyralid	.55	80 b	5 bc	10 b
Clopyralid	1.10	90 a	10 b	15 b
Clopyralid	2.20	95 a	15 b	15 b
Untreated		3 c	3 c	5 b

[1] Means within a column followed by the same letter are not significantly different ($P \leq 0.05$) according to Duncan's multiple range test.

dicamba and the 0.50 and 0.75 lb/acre (0.55 and 0.83 kg/ha) rates of picloram resulted in 100 percent canopy reduction (table 1). Only the 0.25 lb/acre (0.28 kg/ha) rate of picloram resulted in less canopy reduction (80 percent).

Stickyleaf low rabbitbrush response.--Canopy reductions of at least 90 percent resulted from applications of dicamba (3.00 and 4.00 lb/acre, 3.3 and 4.4 kg/ha), 2,4-D (4.00 lb/acre, 4.4 kg/ha), picloram (0.50 and 0.75 lb/acre, 0.55 and 0.83 kg/ha), and clopyralid (1.00 and 2.00 lb/acre, 1.10 and 2.2 kg/ha) (table 1). Lower rates of 2,4-D (2.00 lb/acre, 2.20 kg/ha), picloram (0.25 lb/acre, 0.28 kg/ha), and clopyralid (0.50 lb/acre, 0.55 kg/ha) resulted in 40, 80, and 75 percent canopy reductions, respectively.

Bitterbrush response. The 2.00 lb/acre (2.20 kg/ha) application rates of 2,4-D severely reduced canopy coverage (90 percent). Clopyralid applications of 0.25, 0.50, 1.00, and 2.00 lb/acre (0.28, 0.55, 1.10, and 2.20 kg/ha) resulted in bitterbrush canopy reductions of only 10, 5, 10 and 15 percent (table 2).

Serviceberry response. Application of 2.00 lb/acre (2.20 kg/ha) 2,4-D reduced canopies of serviceberry 100 percent (table 2). None of the clopyralid applications resulted in canopy reductions in excess of 15 percent.

DISCUSSION

Several methods of selective big sagebrush control are presently available to resource managers. Exploiting the phenological differences between big sagebrush and bitterbrush can reduce damage to bitterbrush. Using soil-active herbicides with low-water solubility (such as tebuthiuron) can effectively reduce damage to deeper-rooted species. This may be desirable in the case of bitterbrush, or undesirable in the case of rabbitbrush. Selectivity can be expected to increase with increasing clay content and decreasing precipitation. Placement selectivity, using individual plant treatments, may be a viable alternative for small or critical areas.

Mountain big sagebrush, threadleaf rubber rabbitbrush, and stickyleaf low rabbitbrush can be adequately (90 percent) controlled using 2,4-D, dicamba, picloram, or clopyralid. However, results from these studies, though preliminary, suggest that clopyralid can potentially be used to control these members of the Compositae family while causing relatively little damage to members of the Rosaceae family, such as bitterbrush and serviceberry. Both bitterbrush and serviceberry are often damaged severely by 2,4-D applications. These results and data presented by Tueller and Evans (1969) also suggest that low rates of picloram (0.25 to 0.40 lb/acre, 0.28 to 0.44 kg/ha) could be used to control some rabbitbrush species while only thinning the sagebrush.

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RANGE BRUSH CONTROL WITH GRASLAN[R] PELLETS

J. H. Marion, E. I. Hackett, J. W. Burkhardt

ABSTRACT: Graslan[R] Pellets impregnated with either 10 or 20 percent tebuthiuron by weight were applied to plots on two sites. Five rates from 0.25 to 1.50 pounds per acre (1.28 to 1.68 kg/ha) were distributed on site 1, and three rates of 0.75, 1.0, and 1.50 pounds per acre (0.84, 1.12, 1.68 kg/ha) on site 2. A satisfactory reduction of 78.1 and 81.3 percent, respectively, of Artemisia tridentata was obtained. Chrysothamnus nauseosus was not controlled at any of the rates used. The shallow, wide spread of A. tridentata lateral roots allows this species greater exposure to the pellets; therefore, it is more susceptible to herbicide absorption. Application time was found to be noncritical; response to spring and fall treatments was not significantly different.

INTRODUCTION

Big sagebrush (Artemisia tridentata) and rubber rabbitbrush (Chrysothamnus nauseosus) dominate the ranges of northeastern Nevada, reducing the early season carrying capacity for both wildlife and livestock. Thinning of these shrubs is desirable when the dense stands crowd out more palatable grasses and forbs. Thinning is also desirable where the sagebrush is an unpalatable biotype (Welch and others 1981).

Various herbicides have been used to accomplish this thinning, but most require specific conditions to be effective. One herbicide, tebuthiuron in pellet form, appears to be effective in controlling a wide range of shrubs and trees such as whitebrush, spiny hackberry, and Berlandier wolfberry, found on the mixed shrub ranges of south Texas (Scifres and others 1979). Western juniper (Britton and Sneva 1981), sand shinnery oak (Pettit 1979, Jones and Pettit 1984), huisache (Bovey and Meyer 1978), blackjack oak, winged elm (Shroyer and others 1979), and pinyon-juniper (Clary and Goodrich 1983) also have reportedly been effectively controlled.

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The purpose of this study was to evaluate Graslan[R] (tebuthiuron impregnated pellets) as a method of controlling big sagebrush and rubber rabbitbrush.

MATERIALS AND METHODS

Site 1, selected in the spring of 1980, was in the foothills of the Ruby Mountains, NV at an elevation of 6,000 ft (1 800 m). Annual precipitation average was 9 inches (23 cm) on a shallow soil over a clay pan. Site 2, selected a year later, was 18 miles (28 km) to the southeast at 6,700 ft (2 000 m). Annual precipitation was 15 inches (38 cm), mostly snow, on rocky, deep, well-drained soil of a lateral moraine. Sagebrush density was about equal on both sites. Site 1 had over twice as much rabbitbrush as did site 2. Utah juniper (Juniperus osteosperma), spiny hopsage (Grayia spinosa), and horsebrush (Tetradymia spp.) on site 1 were not found on site 2. Antelope bitterbrush (Purshia tridentata) was found only on the higher site 2.

The plot design was a complete randomized block with three parallel, adjacent replications. Site 1 individual plots were 100 x 100 ft (30.5 x 30.5 m) with a 10-ft (3-m) buffer strip between each plot. There were six treatments and one control plot in each replication, for a total of 21 plots on this site, covering 5.8 acres (2.3 ha). Site 2 was also a complete randomized block with three parallel, adjacent replications of 100 x 100 ft plots, but without the buffer strip between plots. Ten plots were required for each replication to accommodate six spring and three fall treatments plus a control plot. This 30-plot site required 7 acres (2.8 ha).

The Graslan[R] pellets supplied by Elanco were 3 mm in diameter and 5 mm long, averaging 8,000 per pound (Graslan technical manual 1983). The pellets were impregnated with either 10 or 20 percent tebuthiuron designated as 10P and 20P. Untreated blank pellets of the same size were also supplied for making up the correct rates. Elanco suggested a rate of 1 pound active tebuthiuron per acre (1.12 kg/ha) as a midpoint for the rate trials on site 1. Therefore, rates of 0.25, 0.50, 0.75, 1.00, and 1.50 pounds per acre (0.28, 0.56, 0.84, 1.12, 1.68 kg/ha) were prepared for site 1 by weighing out the impregnated pellets and diluting each weight with blank pellets to make up a volume filling a

2-pound coffee can. At site 2 the rates for the spring treatment were 0.75, 1.00, and 1.50 pounds per acre (0.84, 1.12, and 1.68 kg/ha), comparing both the 10P and 20P at each rate. The fall treatment used only the 10P for the 0.75 and 1.00 pound rates and 20P for the 1.50 pound rate. Grams of impregnated pellets used on individual plots at the designated rate per acre are tabulated below.

Lbs/Acre Rate	Percentage concentration	
	20	10
0.25	130	--
0.50	260	--
0.75	390	780
1.00	520	1040
1.50	780	1560

The impregnated pellets and blank pellets were mixed thoroughly and applied to the designated plot with a small, hand-operated, cyclone spreader. One-half of the volume was spread traversing the length of the plot, the remainder being applied crosswise by walking a grid of 10-ft (3-m) increments to accommodate the range of the spreader.

The Graslan pellets were applied to site 1 in March 1980. In April 1981, pellets were applied to the six plots designated for spring treatment on site 2, and in November, the remaining three fall plots were treated. No other work was done on either site, except for random observation, until they were read in October 1983.

Tebuthiuron treatment effects were assessed by establishing three parallel line transects 25 ft (7.5 m) apart in each plot. Starting 25 ft into the plot and extending 50 ft (15 m) towards the opposite boundary, a measuring tape was stretched and anchored just above the plants' canopy. Perennial plants falling under this line transect were recorded by species and measured as inches of live or dead plant material intercepted. Live or dead plants of the major species in a 3-ft wide strip paralleling the transect were also recorded. Cover of annual bromegrass (Bromus tectorum) was estimated at point intercepts at 1-ft intervals along the three transects in each plot.

Ten species of plants were recorded and an additional four noted along the 63 transects on site 1, and 90 transects on site 2. For statistical purposes, only four species were recorded consistently enough to analyze. These were big sagebrush, rubber rabbitbrush, Sandberg bluegrass (Poa secunda) and annual bromegrass. A random block analysis of variance was used to test for differences among treatments.

The variance due to treatment (percentage of dead plants) in the treated plots compared to the control plots was applied to the perennial species. Only live annual bromegrass plants were counted; therefore, the plant counts were used instead of percentage dead.

RESULTS AND DISCUSSION

Herbicide treatments produced significant reduction of big sagebrush compared with the control plots, except for the lowest rate applied on site 1 (0.25 pounds). The 0.75 pound rate was the lowest used on site 2 and big sagebrush reduction was significant for all rates, both spring and fall treatments, regardless of the percentage of active material in the pellets. Rabbitbrush was not controlled and few plants were killed at any of the rates on either site (table 1). At least an 80 percent reduction of rabbitbrush on site 1 and 50 percent on site 2 would have been required for the desired range improvement.

Table 1.--Plant survival percentages

Pounds/acre tebuthiuron	ARTR[1]	CHRY3[2]	POSE[3]
Site 1			
0.25	37.5	83.5	99.3
0.50	25.3*	84.0	89.5
0.75	12.8*	78.5	82.3
1.00	23.3*	85.5	64.9
1.50	9.8**	86.4	53.0
Mean	21.9	84.1	79.0
Control	66.4	90.5	98.4
Site 2			
0.75	25.1*	97.3	52.2
1.00	19.8*	94.2	63.3
1.50	11.6*	84.2	44.3
Mean	18.7	91.7	52.7
Control	85.3	99.9	92.5

* Indicates significant reduction at the 5% level.
** Indicates significant reduction at the 1% level.
1 ARTR = Artemisia tridentata
2 CHRY3 = Chrysothamnus spp.
3 POSE = Poa secunda

Sandberg bluegrass reduction due to the herbicide was not significant at any rate tested. Live annual bromegrass plants were significantly less only at the highest rate (1.50 pounds per acre active tebuthiuron).

Antelope bitterbrush, a desirable species for deer winter range, was found only on site 2 and was not reduced by the tebuthiuron treatments. A total of 65 bitterbrush plants were counted along the 90 transects on site 2 and only five of these were dead, one of which was on an untreated control plant.

The application in March 1980 on site 1 was followed by a very dry period and little effect

of the herbicide was seen 6 months later. The fall of 1981 began a period of above normal moisture that continued until the plots were read in October 1983. It was interesting to note that the herbicide remained effective enough through the long, dry spell of 1980 and 1981 to induce a significant sagebrush reduction after moisture finally came in sufficient quantity to move the material into the root zone.

Site 2 treatments in April 1981 occurred while some snow still remained in sheltered areas, and a 6-inch snow came 2 days later. By the time the fall applications were made in November the results of the spring treatments could be easily seen by the dying sagebrush and hit spots in the understory grass and forbs. Sandberg bluegrass, the major understory species, was quite variable across the plot sites. Zero counts were recorded on several of the transects. More bluegrass was found on site 2 where the spring treatment compared the 10P and 20P (10 and 20 percent active tebuthiuron) pellets. It was found that the 10P killed more grass than the 20P, but the reverse was apparent with the sagebrush where the 20P killed slightly more sagebrush at the same rates per acre of tebuthiuron. Sandberg bluegrass sustained a 41 percent loss with the 10P material and 34 percent with the 20P, an average of all rates. The 20P pellets gave 87 percent control of the sagebrush, and the 10P gave 83 percent. This trend followed through on all treatment pairs, but it was not statistically significant due to the variability of the bluegrass stands on the site (fig. 1). Twice the number of 10P pellets were required to equal the same rate of tebuthiuron, therefore, more hits where grass was killed appeared on the 10P plots. The more concentrated 20P pellets provided a higher lethal dose to the roots of the sagebrush.

A fall treatment on site 2 provided essentially the same results as the spring treatments by the time the plots were read in the fall of 1983. All herbicide rates and concentrations, both spring and fall, provided a significant control of the big sagebrush. No control of the rubber rabbitbrush was found at any of the rates, concentration of pellets, or season of treatment. The rooting habit of the sagebrush makes it particularly vulnerable to this herbicide. Its lateral roots spreading profusely just below the surface, well beyond the plant's canopy, provide a large surface area within which the pellets can fall and still reach the plant's zone of active absorption. This rooting habit is well illustrated by Tabler (1964). The excavated sagebrush plant in the foreground of the photo (fig. 2A) shows the horizontal roots that are in the top few inches of the soil profile. Bovey and others (1978) reported that most of the tebuthiuron residue at any given time was found in the upper 15-cm of the soil.

Rubber rabbitbrush has lateral roots angling downward and not extending much beyond the plant's canopy until deep within the soil. The effect of the herbicide is greatly diluted by the soil before reaching the active root zone of the plant. The photo also illustrates the rooting habit of the rubber rabbitbrush (fig. 2B).

These plants were arranged for photographing at approximately the same distance from each other

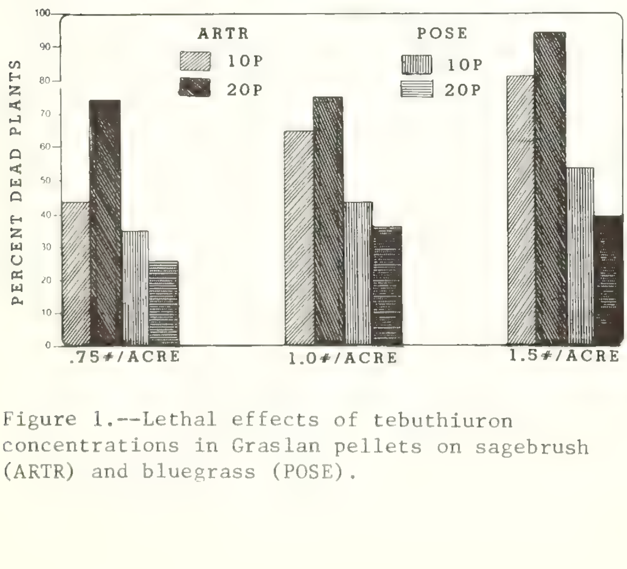

Figure 1.--Lethal effects of tebuthiuron concentrations in Graslan pellets on sagebrush (ARTR) and bluegrass (POSE).

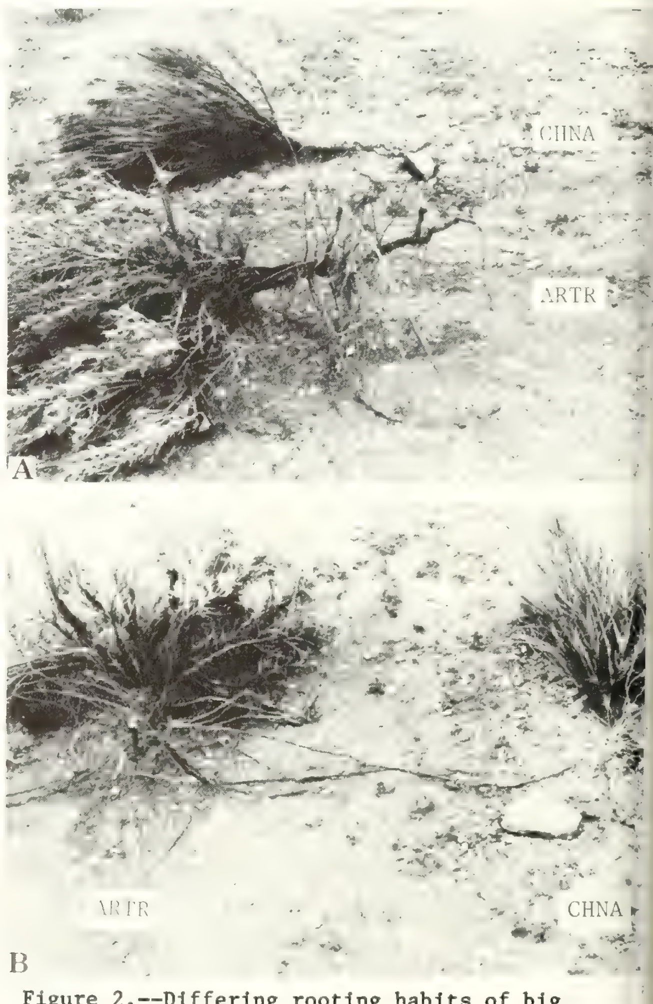

Figure 2.--Differing rooting habits of big sagebrush (ARTR) and rubber rabbitbrush (CHNA).

that they occupied in the soil when growing. The sagebrush roots extended beyond the rabbitbrush plant, but the rabbitbrush roots were not found beyond the plant's own canopy (fig. 2B).

CONCLUSIONS

Graslan is an effective management herbicide for the reduction of A. tridentata. The herbicide was found ineffective in control of rubber rabbitbrush (table 1). The chief advantage of the tebuthiuron-impregnated pellets is that timing of application is not as critical as with foliage spray herbicides. At low concentration (0.5 pounds per acre) most of the grass, forbs, and browse species were preserved. They increase rapidly when sagebrush competition is reduced. The more desirable shrubs such as antelope bitterbrush are not seriously damaged.

Scifres and Mutz (1978) found that although forb production decreased with increasing rates of tebuthiuron, recovery after 3 years was evident. Grass production increased after the first year. Our observations concur with this report.

Tebuthiuron pellets are an excellent management tool for the rancher whose ranges are dominated with big sagebrush. It is effective in thinning sagebrush, allowing the grasses and forbs to increase, thereby providing earlier, longer season, and better balanced forage. There are no secondary effects from the pellets falling in water or from animal waste that includes treated forage. The pellets can be distributed with a minimum of equipment, hand spread from a saddlebag or cyclone seeder as was done on these plots, or by pickup or tractor-mounted spreader. Large acreages can be treated by aerial applications. The pellets can be applied any time that is convenient, except on snow-covered ranges.

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RESPONSE OF AN ALKALI SAGEBRUSH/FESCUE SITE TO RESTORATION TREATMENTS

Stephen B. Monsen and Nancy Shaw

ABSTRACT: The 5-year response of shrubs, broadleaf herbs, and grasses on an alkali sagebrush site to spraying, burning, chaining, disking, and protection from grazing is presented. With the exception of protection from grazing, all treatments reduced shrub density and the vigor of understory species improved. Shrub density and age class did not stabilize within the 5-year period for most treatments. Alkali sagebrush (Artemisia longiloba) plants were susceptible to all treatments. Existing shrubs that were able to survive treatments regrew from new stems not by root sprouting. Recovery of the shrubs and understory plants was aided by unusually high amounts of moisture during years following treatment. Physical alteration of the surface soil by chaining or disking reduced shrub seedling establishment compared to burning or spraying where soils were not disrupted. Perennial bunchgrass and broadleaf forb cover increased slowly after treatment due to low initial density.

INTRODUCTION

Alkali sagebrush (Artemisia longiloba [Osterhout] Beetle) occupies more than 30,000 acres (12 140 ha) of Idaho's Upper Snake River Plain in Blaine and Camas Counties (U.S. Department of the Interior, Bureau of Land Management, Idaho State Office n.d.). Habitat type of these sites has been described by Hironaka and others (1983) as alkali sagebrush/Idaho fescue (Festuca idahoensis Elmer). Stands in good condition support a mixed understory of perennial grasses and annual and perennial forbs, providing valuable forage and cover for sage grouse, antelope, and other wildlife. In this area, alkali sagebrush received light use by cattle and light to moderate sheep use, but deteriorization of understory cover and increases in sagebrush density have resulted from past grazing practices. Although the taxonomic position and site requirements of alkali sagebrush have been studied (Beetle 1960; Tisdale and others 1965; Brunner 1972; Zamora and Tueller 1973; McArthur and others 1979), little research has been conducted on management or manipulation of alkali sagebrush to improve its value for wildlife and livestock.

Alkali sagebrush is distributed over approximately 5,120 mi^2 (1 325 000 ha) from southwestern Montana to northwestern Colorado, along the foothills of the Continental Divide and on scattered sites across southern Idaho a Oregon and northern Utah and Nevada at elevations between 4,500 and 8,000 ft (1 370 t 2 450 m) (USDI Bureau of Land Management and USDA Soil Conservation Service 1976; McArthur and others 1979). It is distinguished from other low sagebrush by its dark green spreadin branches to 1.5 ft (4.5 dm) tall, large flowering heads, and early phenology. Floweri heads vary from 0.12 to 0.2 inches (3 to 5 mm) wide, and flowering and fruiting dates are approximately 1 month earlier than for other low sagebrushes (Beetle 1960; McArthur and others 1979; Blaisdell and others 1982).

Edaphic factors limit the distribution of alkal sagebrush. It characteristically grows in small, sharply defined stands on rocky claypan soils with fine-textured surface horizons and strongly developed agrillic B horizons within or 2 ft (0.3 to 0.6m) of the surface (USDI Bureau of Land Management and USDA Soil Conservation Service 1976; Blaisdell and othe 1982). Beetle (1960) associated alkali sagebrush with highly alkaline soils. Howeve Passey and Hugie (1962), Robertson and others (1966), Passey and others (1982), and Tisdale and others (1965) found the pH of alkali sagebrush sites to range from slightly acidic slightly basic. Therefore, Blaisdell and oth (1982) have proposed "early sagebrush" as a m appropriate common name for the species.

Surface soils of alkali sagebrush sites are temporarily saturated in the spring, but soil moisture is rapidly lost through evapotranspiration. Robertson and others (19 found that soils on an alkali sagebrush site North Park, CO, limited root penetration and moisture availability. They concluded that o a "low-producing plant community of alkali sagebrush and other shallow-rooted, drought-adapted shrubs, grasses, and forbs a able to survive under these conditions." Adapted species quickly complete their vegetative and reproductive phenologies or, the case of annuals, their entire life cycle early in the season while soil water is available. Perennial species may respond to a rains.

Paper presented at the symposium: Biology of Artemisia and Chrysothamnus, Provo, UT, July 9-13, 1984.

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reatment of alkali sagebrush stands to improve nderstory herbs yet retain some shrubs requires elective treatment. Hironaka and others (1983) ecommended chemical and mechanical methods that ould be implemented with a minimal amount of quipment breakage. Eckert and Evans (1968) chieved an average of 96 percent control of lkali and low sagebrush (Artemisia arbuscula utt.) in Nevada by spraying with 2,4-D. Dominant limax perennial grasses showed a production esponse 2 years following treatment with Sandberg luegrass (Poa sandbergii Vasey) demonstrating the reatest initial response. The most successful reatments were on high potential sites in fair ondition. Blaisdell and others (1982) reported hat mechanical treatments have been successfully mplemented on dwarf sagebrush sites, but ecommended treatment of only those areas with the reatest production potential. Prescribed burning as been attempted on alkali sagebrush sites only nfrequently; the understory is normally not heavy nough to carry a fire (Blaisdell and others 982).

ne goal of this study was to evaluate and compare ontrol of alkali sagebrush and the response of ative understory species on a south-central Idaho ite to: (a) spraying with 2,4-D, (b) chaining,) disking, (d) burning, and (e) protection from ivestock grazing.

UDY AREA

acon Flat is an undulating basaltic lava plain ocated along the southeastern edge of Camas rairie, Camas County, ID. Elevation ranges from 800 to 5,500 ft (1 463 to 1 677 m). Slopes are nerally between 0 and 8 percent, but may be as gh as 20 percent. Climate is semiarid with cold nters and hot, dry summers. Annual rainfall erages 14.6 inches (36 cm) (table 1) with 89 rcent falling between October and June, largely the form of snow and spring rain. Wide uctuations in annual percipitation are typical. om 1973 to 1983 total annual precipitation ried from 8.9 to 26.8 inches (23 to 68 cm). an annual temperature is 42 °F (5 °C) with erage winter lows of -23 °F (-31 °C) and summer ghs of 96 °F (35 °C). The frost free season erages 68 days, from June 22 to September 1.

ils are Magic montmorillonitic frigid Vertic rocrepts and Manard fine montmorillonitic igid Argic Durixerolls derived from basaltic siduum (USDI Bureau of Land Management and DA Soil Conservation Service 1976). Surface yers are very stony, and there are occasional tcrops of basalt bedrock. Both soils are derately deep and moderately well drained with w permeability (USDI Bureau of Land Management d USDA Soil Conservation Service 1976; Case 31). The high shrink-swell capacity and asonal perched water table that develops on e strongly developed claypan soils restricts oting depth to 20 to 40 inches (51 to 102 cm).

oductivity is limited by soil conditions and e short growing season. The dominant habitat e of Macon Flat is alkali sagebrush/Idaho fescue. Alkali sagebrush is virtually the only shrub growing on these sites. Bluebunch wheatgrass (Agropyron spicatum) [Pursh] Scribn. & Sm.), Idaho fescue, bottlebrush squirreltail (Sitanion hystrix [Nutt.] J.G. Sm.) and Columbian needlegrass (Stipa columbiana Macoun) are major perennial grasses. Perennial forbs include narrowleaf pussytoes (Antennaria stenophylla Gray), longleaf phlox (Phlox longifolia Nutt.), Hood's phlox (Phlox hoodii Richards.), and Wyeth's eriogonum (Eriogonum heracleoides Nutt.), while littleflower collinsia (Collinsia parviflora Dougl. ex Lindl.) and Brewer's navarretia (Navarretia breweri [Grey] Greene) are common annuals. Isolated patches of basin big sagebrush (Artemisia tridentata Nutt. ssp. tridentata) and antelope bitterbrush (Purshia tridentata [Pursh] DC) occur on ridges or hills with deep, well-drained, loamy soils. Fuzzy sagebrush (Artemisia papposa Blake & Cronq.) inhabits intermittent drainageways (USDI Bureau of Land Management and USDA Soil Conservation Service 1976).

Prior to 1972, the Macon Flat allotment was grazed by cattle and sheep in the spring and early summer and by sheep in the fall. Season of use was restricted and a modified three-pasture rest-rotation system was instituted in 1972. In 1978, cattle grazing was restricted to May 1 to May 22 or May 22 to June 15. Sheep graze the area in the spring and fall with spring grazing confined to the use pastures. From 1972 to 1982 grazing by sheep amounted to 7 to 56 percent of the total use. The Spring Creek pasture, which includes the study exclosure, is in the most depleted condition with about 14 acres (5.7 ha) required per AUM (Boltz n.d.).

METHODS

In 1978, an 80-acre (32.4-ha) tract of the Spring Creek Pasture, Macon Flat allotment was fenced to exclude livestock. Spraying with 2,4-D, chaining, disking, and burning were performed on 300 by 1,000 ft (91.5 by 305 m) plots. A control plot of the same size was established adjacent to treatment plots. One-half of each treated plot was seeded using a rangeland drill. The unseeded portion of each plot was allowed to recover through natural successional changes. This report describes the response of treated areas that were not seeded. Response of the seeded treatments will be presented in a separate publication. The treatments applied included:

Spraying.--The first spraying was completed on June 13, 1979, with a ground spray unit. Two pounds per acre (0.9 kg per ha) of low-volatile 2,4-D ester was applied with water as a carrier. However, by this date the sage had completed most of its vegetative growth and the spray was ineffective. Respraying by helicopter on May 2, 1980, using the same herbicide and application rate was successful.

Table 1.--Weather data for Fairfield, Camas County, ID, during the 1978-83 study period and 10 year averages

Category	1978	1979	1980	1981	1982	1983	Mean 1973-8
	Year						
	Inches						
Precipitation							
January 1 - March 31	6.5	5.0	5.9	3.0	7.0	8.9	5.4
April 1 - June 30	2.5	2.0	3.7	5.1	2.9	3.6	2.6
July 1 - September 30	3.7	3.3	2.7	0.4	4.8	3.6	6.0
October 1 - December 31	1.8	4.8	4.5	9.5	3.3	10.7	3.7
Annual	14.6	14.3	16.8	18.0	18.0	26.8	14.6
	°F						
Temperature							
High	96	95	97	95	95	98	96
Low	-20	-27	-23	-12	-32	-40	-23
Average	42	42	42	44	40	41	42
	Days						
Growing season							
32 °F	[1] 52	84	69	23	103	20	68
28 °F	93	135	111	24	124	117	98

[1] Number days between last spring and first fall occurrence.

Chaining.--The area was double chained in October 1978, using an 80-lb (36-kg) smooth-link chain drawn by two D-9 Caterpillar tractors.

Disking.--Treatment was completed with a brushland plow in October 1978. Grass seed was mistakenly seeded over portions of the area to be left unseeded. Presence of the seeded grass was felt to interfere with the recovery of native vegetation. Consequently, this treatment was not included in comparative analysis.

Burning.--Burning was conducted in mid-June 1978, using a thermal brush burner (Davis 1978). The burner heads were held 2.5 to 3 ft (0.8 to 0.9 m) above the shrubs to ignite and burn the plants and understory. Temperatures at the heads ranged from 2,000 to 2,150 °F (1 093 to 1 177 °C). The burner was drawn through the area at about 3 mi/h (0.8 km/h), burning strips approximately 12 to 14 ft (3.6 to 4.3 m) wide. Fires frequently burned about 20 to 30 ft (6 to 9 m) into the surrounding vegetation before burning out.

Control.--No seeding or plant control methods were employed.

Age class structure, percent live crown cover, and density of alkali sagebrush and cover of all grass and forb species, litter, and bare ground were determined prior to treatment. Evaluations were repeated 1 and 5 years following treatment--1979 and 1983. A single evaluation of the sprayed area was completed in 1983, 4 years following treatment. Data were collected in late June or early July.

Ten 50-foot transects were randomly placed in each treatment. Percent live crown, age class, height, and crown measurements were determined for each shrub rooted within a 4.4-ft (1.3-m) belt centered on the transect line. Ten 10.8-ft^2 (1-m^2) circular plots were randomly located along eac transect line. Percent cover of all species, bare ground, litter, and rock within each circular plot were estimated ocularly. Permanent photopoints were established and rephotographed at each sampling date. All st plots and transects were permanently marked f future sampling and observation.

RESULTS AND DISCUSSION

Response of Alkali Sagebrush

In 1979, 1 year following treatment, the alka sagebrush population on the control plots consisted of approximately 74 percent mature, percent decadent and 1 percent immature plant (table 2). By 1983 the total number of alkal sagebrush plants on these plots had increased nearly 30 percent with a substantial alterati of age structure. Numbers of immature plants and seedlings increased to about 12 percent o the total; this could be attributed to a combination of protection from grazing and weather conditions. All years of the study period received at least normal precipitatio while precipitation for 1980 to 1983 was fro to 84 percent above average. This might have resulted in high seed production, improved germination and seedling emergence, and great seedling vigor. Untreated areas supported o a light understory of herbaceous plants at t beginning of the study that apparently was n prohibitive to shrub seedling establishment. A 25 percent increase in numbers of mature plants between 1979 and 1983 may have result both from growth of plants recorded as immat at the beginning of the study and recovery o decadent shrubs. Number of decadent shrubs decreased 33 percent between 1979 and 1983.

'able 2.--Mean number of alkali sagebrush plants by age class and treatment at Macon Flat; standard error of mean within parentheses

ge class	Sprayed	Burned	Chained	Control
	----------No. shrubs/acre----------			
eedlings				
979	-	709(466)a	142(81)ab	0b
983	0	284	0	203(122)
mmature				
979	-	729(284)	365(122)	142(61)
983	689(223)ab	425(142)b	486(203)b	1,479(344)a
ature				
979	-	5,977(810)	5,126(1,175)	8,205(973)
983	486(203)c	3,039(648)b	2,026(608)bc	10,799(1,074)a
ecadent				
979	-	770(486)	1,783(1,094)	2,674(446)
983	284(162)b	4,194(871)a	6,058(770)a	1,783(405)b
otal				
979	-	8,185(1,276)ab	7,415(839)b	11,021(932)a
983	1,459(142)c	7,942(648)b	8,570(973)b	14,263(1,094)a

Means in the same row followed by the same letter are not significantly different ($P \leq 0.05$).

nrubs in the decadent category usually support cattered live branches, but a majority of the ain branches are dead. Under protection and ith favorable weather conditions, some of these lants recover to produce more uniform crowns.

n 1979, one year after treatment, total shrub opulations on the burned, chained, and disked lots were reduced by 26, 33, and 65 percent, espectively, compared to the control plot (tables and 3). Reduction in plant numbers on the three reated areas occurred primarily in the numbers of ature and decadent plants. The sprayed area was ot sampled at this time as the treatment had ecently been applied and its effects could not et be evaluated.

though no seedings were reported for the ntrol plots in 1979, there were 709, 180, and 2 per acre (1 752, 445, 351 per ha) on the rned, disked, and chained plots, respectively. e numbers per acre of immature plants recorded 1979 for the control, burned, disked, and ained sites were 142, 729, 461, and 365, spectively (351, 1 801, 1 139, 902 per ha). The w number of seedlings and immature plants in the ntrol plots is not fully understood but may have en related to the below-normal precipitation ring the preceding 12 months. Competition and w seed reserves may also have been involved. duction of competition likely contributed to the gher rates of recruitment on the burned, disked, d chained areas. Burning occurred prior to seed spersal in 1978, but the burn resulted in a very otty kill. Apparently enough seed ripened on burned shrubs or remained in the soil to provide seed source. Seedling establishment may have been enhanced in ash mounds left following combustion of the shrubs as seedlings often appeared in clusters. Although chaining and disking left large patches of ground bare in 1979, the loose soil surface of these areas was not conducive to shrub seedling establishment. In addition, the mechanical treatments may have buried many of the small sagebrush seeds and prevented their germination or emergence. The effects of physical alteration of soil on shrub seedling establishment persisted through 1983.

In 1983 the total number of shrubs remained significantly lower in all treated areas than the control. Total number of shrubs in the sprayed, disked, burned, and chained areas were 10, 32, 56, and 60 percent, respectively, of the control. In 1983, the combined number of seedlings and immature plants in the control area was more than twice as great as in the burned, disked, chained, or sprayed areas (tables 2 and 3). This may have been due to differences in seed production in the treated and control areas or increased competition from rapidly developing understory plants on the treated sites. Precipitation from 1981 to 1983 was well above normal, presumably encouraging establishment of all species on all sites. Between 1979 and 1983 there was a significant shift in numbers of plants from the mature to the decadent category on the disked, burned, and chained areas. The category represented 33, 53, and 71 percent, respectively, of the total populations, compared to 13 percent for the control. This indicates a continued loss of vigor of many plants for several years following treatment. Numbers of plants and age structure

Table 3.--Mean number of alkali sagebrush plants by age class for disk treatment

Age class	Year 1979	1983
	-----No. shrubs/acre-----	
Seedlings	180	20
Immature	461	341
Mature	3,251	2,730
Decadent	0	1,505
Total live plants	3,892	4,596

have not stabilized on the treated sites 4 and 5 years after treatment, and it is still impossible to determine the fate of some mature and decadent plants. Changes in weather conditions following treatment undoubtedly play a major role in ultimate shrub survival and recruitment and corresponding changes in cover and composition of the understory species.

Two factors must be considered when treating to prevent or encourage recovery of alkali sagebrush through natural seedings: (1) surface tillage and (2) competition from associated plants. Treatments that till or bury the small sage seeds can prevent seedling establishment; untilled surfaces are more desirable. Competition reduces seedling establishment.

Few seedlings of alkali sagebrush became established for any treatment except the control during the study period. The number of seedlings and immature plants diminished for most treatments between 1979 and 1983. The resurgence in vigor of herbaceous plants apparently was sufficient to prevent shrub seedlings from becoming established and causing plants weakened by physical treatments to succumb.

Elimination or reduction of alkali sagebrush can be achieved with any of the control methods tested. Spraying provided the greatest reduction in shrub numbers during the first 4 years following treatment. During this same period, shrub density had not stabilized in the burned, disked, or chained plot, and numbers continue to diminish in these areas.

The method used to burn the study plot may not be comparable to a natural or prescribed burn that would likely occur much later in the season. A large number of burned shrubs were able to recover. Plants did not resprout from the base of the crowns, but were able to regrow from the remaining branches and apparently are not as susceptible to physical or physiological damage as the various subspecies of big sagebrush.

Burning can be used to reduce shrub density and is an appropriate technique to use if some shrubs are to be retained. Unless a sufficient understory of herbs is present, burning without seeding may result in a rapid increase of shrub seedlings. However, burning will be difficult to conduct in many alkali sagebrush stands unless understory herbs are present to carry a fire.

After 5 years, total shrub numbers were similar on the burned and chained sites. Although differences were nonsignificant, the number of young plants was lower and decadent plants greater for the chained area. If chaining is employed, removal of shrubs can be regulated using chains with links of different weights and by single or double chaining. Chaining would be particularly effective when plants are dormant and the ground frozen.

Shrub recovery on the disked site was influenced by the presence of seeded grasses. Compared with the 11,021 shrubs per acre (27 233 per ha) on the control plot in 1979, disking reduced shrub numbers in 1983 by 42 percent or 4,596 plants per acre (11 357 per ha) (table 3). Disking was particularly destructive to mature and decadent plants and provided a poor seedbed for alkali sagebrush seedlings.

In all treatments, live but damaged shrubs recovered via regrowth of remaining stems. Basal sprouting or root sprouting did not occur, and shrubs were killed if the main stems were uprooted or cut off. Consequently, treatments are most effective if existing plants are completely killed and live stems are not left to regrow.

Response of Herbaceous Species

In 1983 there were no significant differences in total cover provided by perennial grasses on any of the sites (table 4). On treated sites the native perennial grasses were able to recover through natural resprouting or seeding. Differences between treated and control plots may have been minimized by favorable weather conditions during the preceding 3 years.

Significant differences did exist among treatments in cover provided by several perennial grass species. Bottlebrush squirreltail provided greater cover on all treatments than on the control, but significantly so only on the sprayed plots. Bottlebrush squirreltail is a short-lived perennial that invades open sites quickly. Other perennials do not respond as rapidly but may slowly increase in density. Idaho fescue appears to be more sensitive to damage by mechanical tillage than the other perennial grasses present. In 1983 its cover remained significantly lower on the sprayed and chained areas than on burned or controlled sites.

Most perennial grasses are adapted to specific sites. Bluebunch wheatgrass and Thurber needlegrass (*Stipa thurberiana* Piper in Scribn. are more prevalent on the deeper well-drained soils. Idaho fescue, Sandberg bluegrass, and Nevada bluegrass (*Poa nevadensis* Vasey in Scribn.) are more common on the shallow, rocky soils. Chaining was more damaging to the perennial grasses occurring on shallow soils than deep soils, while burning was generally less effective on shallow sites. Fewer grasses and broadleaf herbs survived disking than any

Table 4.--Percent (standard error of mean in parentheses) at Macon Flat in 1983

Cover type	Spray	Burn	Chain	Control
Annual grasses	0.6(0.2)	0.5(0.5)	0.3(0.2)	0
Perennial grasses	[1]15.7(2.9)	12.0(1.3)	11.7(1.6)	12.2(1.3)
Festuca idahoensis	0.3(0.1)b	3.6(1.1)a	0.4(0.3)b	3.8(1.1)a
Poa nevadensis	0b	1.0(0.4)a	0.1(0.1)ab	0.4(0.1)ab
Poa secunda	3.4(0.4)a	0.3b	2.2(0.6)a	2.8(0.3)a
Sitanion hystrix	9.4(1.5)a	4.4(0.5)b	5.6(1.0)b	3.0(0.6)b
Stipa thurberiana	2.6(1.1)	1.1(0.4)	3.2(0.7)	1.5(0.9)
Agropyron smithii	0.1(0.1)b	1.4(0.7)a	0b	0b
Other grasses	0	0.1(0.1)	0.3(0.2)	0.6(0.4)
Annual forbs	4.0(0.4)ab	3.3(0.4)b	6.1(1.0)a	4.0(0.7)b
Perennial forbs	11.5(1.1)	8.2(1.7)	13.9(1.8)	14.5(2.9)
Allium spp.	0.1b	0.2(0.4)ab	0.6(0.2)a	0.2(0.1)ab
Arenaria aculeata	3.0(0.4)a	0.5(0.3)c	2.4(0.6)ab	1.6(0.6)bc
Antennaria spp.	0	1.3(0.5)	1.0(0.4)	0.9(0.2)
Eriogonum caespitosum	0.1b	1.7(0.6)a	2.8(0.5)a	2.8(0.7)a
Eriogonum spp.	0.4(0.2)	0	0.6(0.4)	0.8(0.2)
Happlopappus nanus	2.0(0.5)	1.4(0.7)	2.4(1.3)	4.5(2.0)
Phlox spp.	2.0(0.3)	1.7(0.8)	1.3(0.3)	2.0(0.3)
Viola beckwithii	0.2(0.1)c	0.5(0.1)b	1.5(0.2)a	0.9(0.2)a
Astragalus spp.	0.8(0.3)a	0.2(0.2)b	0.1(0.1)b	0.1(0.1)b
Other forbs	1.8(0.6)a	0.1(0.1)b	1.1(0.5)ab	0.4(0.2)b
Shrubs	6.5(0.8)c	27.5(2.3)b	23.5(2.0)b	36.6(1.6)a
Total vegetation	38.3(2.8)c	51.5(2.3)b	55.6(2.2)b	67.3(1.4)a
itter	30.1(3.6)a	20.2(2.0)b	16.8(1.1)bc	14.4(1.9)c
ock/bare ground	32.9(1.9)	32.9(2.4)	34.9(2.0)	29.0(2.3)

[1] Means in the same row followed by the same letter are not significantly different ($P \leq 0.05$).

ther treatment. The heavy disk plowed all urfaces. However, the treatment did not ompletely eliminate any species.

heatgrass brome was the only annual grass to ppear on all plots. Following disturbance it did ot increase noticeably, providing less than 1 ercent cover on all areas in 1983. Consequently, t did not interfere with recovery of native pecies.

ne percent ground cover for native annual roadleaf forbs increased on the disked, and hained treatment, but not on the burned or prayed treatment. These treatments likely rovided better microsite conditions for invasion nd establishment. Nearly all species provided ery low amounts of cover with the totals for all nnual forbs ranging from 3.3 to 6.2 percent on he various treatments.

over provided by perennial forbs did not vary gnificantly among treatments. Nearly all pecies present in the area occurred in each eatment where microsites permitted, but in low ercentages, generally totaling between 0 and 3 ercent. Response to treatment is difficult to assess due to the low percentages, but in general no species were lost or increased markedly following treatment (see Blaisdell and others 1982; Eckert and others 1972).

The low density and pattern of distribution of most broadleaf herbs and some grasses must be considered in evaluating the success or usefulness of each treatment. With the exception of bottlebrush squirreltail, few seedlings of the perennial species have yet appeared. Increases in density of most native grasses and broadleaf herbs resulted from enlargement of existing crowns or spread by rooting. The low numbers of new seedlings may be due to a number of factors:

1. Native herbs occurred in low densities prior to treatment, producing only low quantities of seeds. Unless adequate number of understory plants are present at the time of treatment, recovery or improvement occurs very slowly. Few perennial forbs or grasses have invaded many exposed sites in the chained or sprayed areas. New seedlings are not plentiful in any treatment.

2. Many plants require specific site conditions and occupy only restricted areas.

Plants spread slowly among the scattered adapted sites.

3. Some desirable species (bluebunch wheatgrass, Idaho fescue, and most species of Stipa) do not have vigorous seedlings and recovery is often quite slow.

If the recovery is to be based on the response of native herbs, treatments that destroy understory plants should not be used. With the exception of disking, treatments were not very disruptive. Existing plants respond by enlargement of the crowns, rooting, and new seedlings. As existing plants improve in vigor, seeds are produced to repopulate the site. Seedling spread may not occur for a number of years until a seed bank can be rebuilt. Recovery of Idaho fescue was particularly slow on all treatments; plants regrew and reseeded more slowly than most other grasses. Bluebunch wheatgrass plants regrew quickly, but spread very slowly by seedlings. Managers may expect most native perennial grasses to require several years to recover following vegetation treatment. Although the total cover of grasses can be expected to improve for most treatments, some desirable species may not recover for many years. Management should be designed to accommodate this response.

CONCLUSIONS AND RECOMMENDATIONS

Alkali sagebrush sites that support a good component of understory herbs provide excellent livestock forage during the early spring and fall--vital grazing periods. To be cost effective, improvement of the herbaceous understory of depleted sites must result in a substantial increase in herbage production. This has not occurred for any treatment, and seeding following site preparation appears necessary to improve areas that are void or sustain remnant numbers of herbs.

Autenreith (1981) emphasized the need for manipulation practices designed to enhance degraded sagebrush habitats for both livestock and wildlife. He recommended treatments that reduce sagebrush density and increase both grass and forb production for sage grouse habitats. With the exception of protection from grazing, all treatments reduced shrub density, but understory herbs have not recovered sufficiently. Shrub density has recovered from all treatments except spraying, and may prevent further increase of herbs. Autenreith also suggested that treatments resulting in total shrub elimination be restricted to selected patches or strips producing a mosaic of shrub and grasslands. Disking, chaining, and spraying are procedures that can be used to treat specific irregular tracts. Kindschy and others (1982) and Yoakum (1968) described suitable antelope habitat as supporting one-third each of grasses, forbs, and shrubs with a height of 24 inches (61 cm) or less, ground cover of about 50 percent, and production of 500 to 1,000 lb/acre (563 to 1 125 kg/ha). Response of herbaceous understory has not yet achieved these figures. Consequently, extensive treatments of depleted sites are not recommended unless an adequate understory of herbs is present for recovery or artificial seedings is part of the treatment.

The method ultimately used to treat large areas depends on the costs involved, density of understory species, and wildlife and livestock uses. Several major considerations in selectin an appropriate treatment include:

1. Providing protection from livestock grazing without additional treatment may be beneficial, but the community composition, particularly shrub density, would be extremely slow to change. The time required would not be acceptable for most management purposes.

2. Burning can be effective, but only if a sufficient understory is present to carry the fire. A rapid increase in alkali sagebrush could occur unless controlled by competition with understory plants.

3. Spraying is an effective method for killing existing shrubs. It can also be an effective method of controlling shrub reestablishment if the understory is able to respond and provide competition with shrub seedlings. Spraying was no more detrimental to the survival of broadleaf herbs than other treatments. Broadleaf herbs, particularly mat-forming species, recovered surprisingly well.

4. Spraying must be completed early in the season (prior to May 20, at Macon Flat) before alkali sagebrush completes most of its vegetative growth. Spraying early in the seas also increases the chance of survival for some broadleaf herbs as the understory plants are n in full production at this time and are not damaged greatly by the herbicide. Spraying ca be recommended if an adequate quantity of understory species is present and regulatory measures are satisfied.

5. Chaining effectively reduces shrub density. Heavy chains can be used to remove most plants regardless of age or size. Many dense stands of alkali sagebrush support a preponderance of mature and decadent plants. Chaining in late fall and winter will kill these plants. Chaining is generally less destructive to the understory plants than spraying and would be more useful in retaining some alkali sagebrush. Both methods are adapt to treatments that include seeding.

6. Disking is most frequently employed to treat low and alkali sagebrush. The technique usually kills a high percentage of shrubs and understory herbs. Recovery of the herbs requires a longer period than for other treatments. This practice is acceptable if significant reduction in shrub density is desired to accommodate seeding.

7. Chaining and disking are useful techniques to prepare a seedbed and facilitat artificial seeding. The equipment can be adjusted or modified to enhance site preparation.

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INTERSEEDING SELECTED SHRUBS AND HERBS ON MINE DISTURBANCES IN SOUTHEASTERN IDAHO

Bland Z. Richardson, Stephen B. Monsen, and Diane M. Bowers

ABSTRACT: Mountain big sagebrush, rubber rabbitbrush, and antelope bitterbrush were successfully established from seed in revegetating a mine disturbance in southeastern Idaho. Grazing and competition from seeded herbs were found to significantly decrease shrub density, particularly antelope bitterbrush. Increasing the shrub seeding rate from 4 to 50 lb/acre (5 to 56 kg/ha) resulted in greater numbers of shrubs, but differences varied by species and treatments. Seeding methods and rates are discussed. Recommendations based on the results are made.

INTRODUCTION

Shrubs and herbs are desirable components for revegetation of mined areas. Benefits derived from their use include: enhanced forage yields and ground cover (Medin and Ferguson 1972; Clarke and DePuit 1981; Ferguson and Frischknecht 1981); promotion of ecosystem processes such as accumulation of litter, nutrient cycling, and soil stability (McArthur 1981; McKell and Van Epps 1981); enhanced animal and wildlife habitat; and increased livestock and wildlife forage (Monsen and Christensen 1975; McArthur 1981).

However, few shrubs and herbs are adapted to semiarid mine disturbances and only a small number of these have been evaluated for use in revegetation of those mined areas (Monsen and Richardson 1984). Further, results are often erratic due to a lack of satisfactory planting equipment (Monsen and Shaw 1983). Most equipment that has been used was developed for planting grasses and is not capable of handling trashy seeds or a mixture of different size seeds.

Mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), rubber rabbitbrush (*Chrysothamnus nauseosus*), and antelope bitterbrush (*Purshia tridentata*) are useful plants for disturbed sites. However, seeds of the first two species are difficult to clean and usually are sold wit[h] a high percentage of inert material. Seeds are small and difficult to regulate in most seeding devices. In contrast, seeds of antelope bitterbrush are large, easily cleaned, and seed freely. When they are seeded in a mixture, a carrier is often needed to regulate seeding rates and this is often not satisfactory.

Grazing is an additional factor affecting revegetation success in some areas. Young plants are adversely affected not only by grazing, but also by trampling (Whittaker 1953; Plummer and others 1968). Despite these effects, "...almost no research has been conducted on improved practices for grazing of land reclaimed after mining" (Power 1978).

This study investigated the suitability of seeding mountain big sagebrush at different rates with herbs on a mine disturbance in southeastern Idaho. Specifically, the study ha[d] three objectives: (1) to evaluate the capability of the Brillion grass-seeder to plan[t] a mixture of shrubs and herbs; (2) to determine the "best" seeding rate to establish a diverse mixture of shrubs and herbs; and (3) to evaluat[e] the influence of livestock grazing (cattle) on plant establishment and composition.

LOCATION

Studies were established at the Gay Mine, a phosphate mine near Pocatello, ID, at an elevation of 5,600 feet (1 707 m). Situated in the northeastern extremity of the Great Basin Desert, average annual precipitation is approximately 11 inches (28 cm). Vegetation is characterized by Saskatoon serviceberry (*Amelanchier alnifolia*), mountain big sagebrush, antelope bitterbrush, and rubber rabbitbrush. Aspen (*Populus tremuloides*) is encountered in small restricted areas. In addition to minerals, principal resources of the area are watershed, game habitat, and livestock forage.

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METHODS

The research plantings were established in a large valley fill in which overburden materials had been deposited. Phosphate overburden had been removed from a pit approximately 44 acres (17.8 ha) in size and having an average depth of 250 feet (76.2 m). The total area disturbed as a result of the pit and the overburden backfill was approximately 100 acres (40.5 ha). The study area, approximately 5 acres (2.0 ha) in size, was ripped to a depth of approximately 3 feet (0.92 m), fertilized (16-16-16 at a rate of 580 lb/acre [649.6 kg/ha]), and planted in the fall of 1977. Three separate seed mixtures: (1) combinations of mixed grasses and broadleaf herbs; (2) mixed shrubs; and (3) grass-herb mixture plus shrubs were sown with a Brillion grass-seeder at different seeding rates (table 1) resulting in a total of 10 treatments.

Table 1.--Planting treatments and seeding rates at the Gay Mine

Treatment number	Seeding rate	
	Grass-Herb	Shrubs
	lb/acre	
1	12	
2	18	
3	50	
4	12	4
5	18	4
6	50	4
7	18	20
8		4
9		45
10		50

The Brillion grass-seeder used in this study is more accurately known at the Brillion Turf-Maker. It is designed for accurately seeding grasses and it is an ideal seeder for surface mine rehabilitation work where the spoil material has been previously ripped and harrowed.

The Turf-Maker has two sets of rollers. The front set crushes lumps and forms a firm seedbed. Seeds are metered into the seedbed with a hopper that is mounted between the front and rear sets of rollers. The rear rollers split the shallow ridges formed by the front rollers and firm the soil around the seed thereby ensuring good hydraulic conductivity of the soil with the seed. Using this equipment and various size seed there will always be some of the seed at the proper depth for best germination.

There are two common misconceptions about using the Brillion on rocky soils. One is that it will not plant in rocky materials. The second is that rocks break the rollers, thereby requiring a great deal of time and effort to change the broken rollers.

The first complaint is not valid except when the Brillion is misused. The second complaint is sheer misuse and abuse of equipment. Speed is the greatest enemy of the Brillion when used in rocky spoils. The larger the rocks, the slower the seeder must travel. The Brillion used by the authors was purchased in 1972 and has seeded under the most severe rocky conditions and never required any repair. It is not uncommon for the Brillion to seed over spoil materials that have been deep-ripped, harrowed and have rocks six inches to one and one-half feet in diameter.

The grass and shrub species used are listed in tables 2 and 3. Treatments 1, 2, and 3 were planted with the grass-broadleaf herb mixture, but at three different seeding rates (12, 18, 50 lb/acre [13, 20, and 56 kg/ha] respectively) and with no shrubs. Treatments 4, 5, and 6 also were seeded with the grass-broadleaf herb mixture at 12, 18, and 50 lb/acre (13, 20, and 56 kg/ha); shrubs were simultaneously seeded at 4 lb/acre (5 kg/ha) in these three treatments. Treatment 7 was seeded at 18 lb/acre (20 kg/ha) of mixed grass-broadleaf herb and 20 lb/acre (22 kg/ha) of shrubs. Treatments 8, 9, and 10 were seeded with shrubs only at 4, 45, and 50 lb/acre (5, 50, and 56 kg/ha). The percent composition of species seeded in both the grass-broadleaf herb and shrub mixtures remained consistent (tables 2 and 3).

The research area was fenced so that four-fifths of each treatment was protected from cattle grazing, while the other one-fifth was exposed. Annual assessments determined percent ground cover, species density, and production for each treatment in the grazed and protected area. Herbaceous vegetation was sampled using 10 randomly placed 1 by 2 feet (0.33 by 0.66 m) plots in each treatment. Five transects, 5 by 15 feet (4.6 by 13.8 m) were randomly placed in all shrub seeding treatments to record shrub numbers and annual growth features.

RESULTS AND DISCUSSION

Grasses and Broadleaf Herbs

The percent herbaceous ground cover (grasses and broadleaf herbs) for the different grass-broadleaf herb seed mixture treatments recorded in 1984, 7 years after planting, is presented in table 4. The percent ground cover of seeded grass differed little between grazed and protected areas for each treatment. In contrast, the percent ground cover of seeded herbs was distinctly less on grazed areas. Alfalfa (Medicago sativa) was the most prevalent broadleaf herb and received heavy grazing. Consequently, it was more abundant in the protected areas. Further, the protected areas had less bare ground than the grazed areas because the lack of grazing pressure allowed the plants to attain larger size and a greater accumulation of litter.

Increasing the grass-broadleaf herb seeding rates from 12, 18 or 50 lb/acre (13, 20 and 56

kg/ha) did not result in an increase in ground cover for either the grazed or protected treatments (table 4). The lack of any large difference between the three rates 7 years after planting suggests that seeding the area at 12 lb/acre (13 kg/ha) would be suitable unless more total cover is needed the first year for erosion control.

The percent herbaceous ground cover for the grass + shrub seed mixture treatments is listed in table 5. The amount of ground cover for both grasses and broadleaf herbs was greater on the protected treatments. As with the grass seed mixture, somewhat less variability in ground cover occurred among the grazed treatments. The high variability in the amount of ground cover on the

Table 2.--Grasses and broadleaf herbs planted and seeding rates for all treatments

Species seeded	Purity	Germination	PLS[1]	No seeds per lb	Pct of mixture (weight)	Treatments 1	2	3	4	5	6	7
	- - - Percent - - - - -					Pounds pure live seed (PLS) - - - - - Planted per acre - - - - - -						
Grasses												
Agropyron cristatum	95	90	85.5	319,660	15.6	1.60	2.40	6.67	1.60	2.40	6.67	2.40
Agropyron intermedium	96	90	85.5	88,110	26.0	2.67	4.00	11.12	2.67	4.00	11.12	4.00
Agropyron riparian	95	90	85.5	137,830	5.2	.53	.80	2.23	.53	.80	2.23	.80
Agropyron siberian	97	90	87.3	212,855	5.2	.55	.82	2.27	.55	.82	2.27	.82
Agropyron smithii	86	80	68.8	149,210	5.2	.43	.64	1.79	.42	.64	1.79	.64
Bromus inermis	90	85	76.5	105,980	5.2	.48	.72	1.99	.48	.72	1.99	.72
Dactylis glomerata	95	90	85.5	600,000	5.2	.53	.80	2.23	.53	.80	2.23	.80
Festuca idahoensis	95	90	87.3	1,050,000	6.1	.55	.96	2.67	.55	.96	2.67	.96
Festuca ovina duriuscula	96	85	81.6	633,520	10.4	1.02	1.53	4.25	1.02	1.53	4.25	1.53
Psathyrostachys junceus	90	70	63.0	130,760	5.2	.39	.59	1.64	.39	.59	1.64	.59
Broadleaf Herbs												
Linum lewisii	90	85	76.5	278,280	1.3	.12	.18	.50	.12	.18	.54	.18
Medicago sativa	99	82	81.2	213,760	10.4	1.01	1.52	4.22	1.01	1.52	4.22	1.52

[1]PLS=Pure live seed.

Table 3.--Shrubs planted, seed features, and seeding rates for all treatments

Species	Seed features: Purity	Germ.	PLS[1]	No. seed per lb	% seed mixture	Amount seed planted (PLS[1]/AC) --Treatments-- 4 (4 lb) bulk	5 (4 lb) bulk	6 (4 lb) bulk	7 (20 lb) bulk	8 (4 lb) bulk	9 (45 lb) bulk	10 (50lb bulk
Artemisia tridentata	12	80	9.6	2,575,941	0.08	0.08	0.08	0.08	0.42	0.08	0.95	1.06
Chrysothamnus nauseosus	80	78	62.4	693,220	3.0	0.07	0.07	0.07	0.37	0.07	0.84	0.95
Purshia tridentata	95	85	80.7	15,370	32.0	1.03	1.03	1.03	5.16	1.03	11.62	12.9
(Carrier)					43.0							

[1]PLS=Pure live seed.

Table 4.--Percent ground cover for grass-broadleaf herb seeded treatments, 1984[1]

Cover	Treatment 1 (12 lb/acre)		Treatment 2 (18 lb/acre)		Treatment 3 (50 lb/acre)	
	Grazed	Prot.	Grazed	Prot.	Grazed	Prot.
Seeded grass	33.4	38.4	29.8	21.2	27.8	30.9
Seeded broadleaf herbs	35.2	44.6	26.4	46.0	16.2	32.6
Total liver cover	68.6	83.0	56.2	67.2	44.0	63.5
Bare ground	21.4	5.2	41.6	9.4	34.4	5.8

[1]Totals do not equal 100 percent since litter is not included and storied cover was recorded.

Table 5.--Percent ground cover for grass-broadleaf herb and shrub seed mix treatments, 1984[1]

Cover	Treatment 4 (12/4)[2]		Treatment 5 (18/4)		Treatment 6 (50/4)		Treatment 7 (18/20)	
	Grazed	Prot.	Grazed	Prot.	Grazed	Prot.	Grazed	Prot.
Seeded grass	39.0	35.0	28.2	37.2	21.6	32.3	23.4	39.4
Seeded broadleaf herbs	21.8	37.2	37.0	43.0	36.0	60.6	22.0	35.0
Seeded shrubs	.5	7.8	.3	.1	20.3	47.7	.4	.5
Bare ground	24.6	6.6	18.8	2.2	29.8	2.2	41.6	11.6

[1]Totals do not equal 100 percent since litter is not included and storied cover was recorded.
[2]Grass/shrub seed mix, pounds per acre.

protected treatments was probably due to the aggressive growth of alfalfa.

Where herbs and shrubs were seeded together, the major difference in herbaceous ground cover appeared to be due to grazing, not seeding rate (tables 4 and 5). Comparison of the two tables shows that addition of shrubs to the seed mixture did not alter the amount of herbaceous ground cover. Further, increasing the seeding rates did not change the proportion of the plants seeded.

Shrubs

With protection from grazing a satisfactory number of mountain big sagebrush plants were able to establish when grasses-broadleaf herbs were seeded at the lowest rate (12 lb/acre [13 kg/ha]) and shrubs were seeded at 4 lb/acre (5 kg/ha, table 6. Slightly over 800 plants per acre (1 976/ha) were recorded in the protected area compared to 54 plants (133/ha) in the grazed portion. Physical damage to the seedbed by livestock perhaps accounted for some decrease in numbers between grazed and protected sites. However, even with protection, mountain big sagebrush plants were unable to compete with the herbaceous plants when the grass-broadleaf herb seeding rates were increased to 18 or 50 lb/acre (20 to 56 kg/ha) and the shrubs seeded at 4 lb/acre (5 kg/ha), treatments 4 and 5, (table 6). Apparently the herbaceous plants provided sufficient competition to prevent the initial establishment of this shrub. With grazing a few mountain big sagebrush plants were able to establish with the higher grass-broadleaf herb seeding rates. Grazing appeared to reduce herb density allowing the establishment of a few shrubs.

With protection, rubber rabbitbrush plants were also able to establish when seeded in mixtures with herbs if the grass-broadleaf herb rate was at 12 lb/acre (13 kg/ha) and shrubs at 4 lb/acre (5 kg/ha). The number of rubber rabbitbrush plants decreased as the grass-broadleaf herb mixture seeding rate was increased from 12 lb/acre (13 kg/ha) to 18 and 50 lb/acre (22 and 56 kg/ha); see table 6. With grazing, no rubber rabbitbrush plants occurred regardless of the grass-broadleaf herb seeding rates. Apparently rubber rabbitbrush plants were susceptible to grazing impacts including foraging and trampling.

When the seeding mixture was increased to 18 lb/acre (22 kg/ha) of grass-broadleaf herbs and 20 lb/acre shrubs (22 kg/ha), the numbers of both mountain big sagebrush and rubber rabbitbrush increased dramatically (table 6). Approximately 3,500 and 4,500 mountain big sagebrush plants per acre (8 648 and 11 119/ha) occurred in the grazed and protected site, treatment 7. The increased numbers of mountain big sagebrush plants in the protected site demonstrate the ability of the shrub to survive with herbaceous competition. Rubber rabbitbrush plants were also able to compete with the herbs

Table 6.--Number of shrubs per acre by treatment, 1984

Treatment	Seeding rate (grass/shrub)	Mt. Big sagebrush Grazed	Mt. Big sagebrush Prot.	Rubber rabbitbrush Grazed	Rubber rabbitbrush Prot.	Antelope bitterbrush Grazed	Antelope bitterbrush Prot.
	lb/acre						
4	12/3	54	81	0	116	0	0
5	18/4	37	0	9	37	0	0
6	50/4	46	0	0	28	0	0
7	18/20	3,538	4,530	0	2,091	0	0
8	/4		2,207		2,788	0	1,041
9	/45	1,742	7,663	826	929	0	2,091
10	/50	2,439	5,343	939	1,041	0	5,576

in the protected site. No rubber rabbitbrush plants were able to establish if grazing was permitted.

Antelope bitterbrush plants were unable to establish in any treatment when seeded with understory grasses and broadleaf herbs. Regardless of the seeding rates, antelope bitterbrush was unable to successfully compete with the herbs (table 6).

If shrubs were seeded alone without grasses and broadleaf herbs, a substantial increase in shrub numbers occurred for all species (table 6). However, responses were affected by grazing. The number of mountain big sagebrush plants increased from 213 to 2,207 per acre (526 to 5 433/ha) in the protected area when shrubs were seeded at 4 lb/acre (5 kg/ha) with and without grasses-broadleaf herbs. As the shrub seeding rate increased from 4 to 45 or 50 lb/acre (5 to 50 or 56 kg/ha) the number of mountain big sagebrush plants nearly doubled in both the grazed and protected sites. However, nearly twice as many plants occurred in the protected site as the grazed area.

The number of rubber rabbitbrush plants also increased substantially when shrubs were seeded alone. However, increasing the seeding rate of shrubs did not result in an increase in rubber rabbitbrush density (table 6). Slightly fewer plants appeared in the grazed areas for all seeding rates.

In protected treatments where shrubs were seeded without grasses and broadleaf herbs, antelope bitterbrush was able to establish. A significant increase in numbers of plants occurred as the shrub seeding rate was increased from 4 to 45 or 50 lb/acre (5 to 50 or 56 kg/ha), table 6. Slightly over 1,000 antelope bitterbrush plants per acre occurred in the protected area when shrubs were seeded alone at 4 lb/acre (5 kg/ha). The number increased to over 2,000 plants and 5,500 plants per acre (4 942 and 13 590/ha) as the seeding rates were increased to 45 and 50 lb/acre (50 and 56 kg/ha). No antelope bitterbrush plants established in the grazed area when shrubs were seeded alone at any planting rate.

CONCLUSIONS

This study demonstrated that the Brillion grass-seeder is capable of planting a mixture o different sized seeds. Further, it is able to disperse "trashy" seeds such as sagebrush and rabbitbrush when they are seeded alone or in a mixture of other species.

An adequate shrub cover was obtained for all three species on the protected plot seeded onl to shrubs at a rate of 4 lb/acre (5 kg/ha). A satisfactory number of mountain big sagebrush plants were established in both the protected and grazed areas when seeded with herbs at a rate of 18 lb/acre grasses broadleaf herbs, an 20 lb/acre shrubs (20 and 22 kg/ha). Rubber rabbitbrush was also adequately established wh seeded at this rate, but only in the protected area. Therefore, the authors recommend a mixture of 0.17 lb/acre (0.19 kg/ha) pure live seed (PLS) sagebrush, 0.15 lb/acre (0.17 kg/ha PLS rabbitbrush, and 1.0 lb/acre (1.1 kg/ha) P bitterbrush (see table 3). These recommendations are minimum rates based upon shrubs being seeded alone and protected from grazing. Mountain big sagebrush and rubber rabbitbrush can be seeded directly with grasse and broadleaf herbs if the herbs are planted a 12 lb/acre (13 kg/ha). The most advantageous seeding rate for both shrubs when planted with grasses and broadleaf herbs was not determined but appeared to be 0.85 lb/acre (0.95 kg/ha) P for mountain big sagebrush and 0.75 lb/acre (0 kg/ha) PLS for rubber rabbitbrush.

Establishing a mixture of shrubs and herbs can be achieved by seeding the two different group in separate strips (Richardson and Trussell 1980). Since grasses and broadleaf herbs develop much faster and offer serious competition to the young shrubs, the amount of shrub seeds required can be reduced if this separation is practiced.

Areas seeded to shrubs must be protected from grazing during the period of shrub establishment, particularly if seeded to antelope bitterbrush or rubber rabbitbrush. Damage to young shrubs from cattle trampling m be as important as the impact of foraging.

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IRRIGATION BY MINE DISCHARGE WATER AND FERTILIZATION OF BIG SAGEBRUSH:

EFFECTS OF NUTRITIONAL COMPOSITION, PRODUCTION, AND MULE DEER USE

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ABSTRACT: Field plots of Artemisia tridentata (big sagebrush) were irrigated by mine discharge water, irrigated-fertilized, and left untreated (control). Measurements were taken to determine the effects of treatments on plant productivity, mule deer preference, digestibility, and chemical composition of forage. The irrigated-fertilized plants were significantly more productive, preferred by wintering mule deer, and contained higher levels of crude protein, phosphorus, and monoterpenoids. The use of mine discharge water and fertilization could compensate for loss of mule deer winter range through mining by increasing the productivity and nutritive value of the remaining range.

INTRODUCTION

Big sagebrush (Artemisia tridentata) is one of the most common range plants on mule deer winter range in the Piceance Creek Basin of western Colorado's oil shale region. Sagebrush, along with pinyon (Pinus edulis) and juniper (Juniperus osteosperma), provide most of the vegetation biomass in the Basin. The use of big sagebrush, pinyon, and juniper for cover and food is well documented (Leach 1956; Kufeld and others 1973; Hansen and Dearden 1975; Tueller 1979; Cluff and others 1982; Pederson and Welch 1982). Although mule deer intensively inhabit big sagebrush stands during winter in the Piceance Basin, just how much big sagebrush is consumed by deer and sagebrush nutritional value are not well documented. An opportunity to study sagebrush use and its nutritive value for wintering mule deer cam[e] on the Federal Prototype Oil Shale Lease Tract C-b (Cathedral Bluffs Oil Shale Company) during the spring of 1980. In an attempt to dispose of excess mine water, employees of Tract C-b installed a sprinkler irrigation system on a big sagebrush-dominated deer winter range. Several plots within the irrigated area were fertilized wit[h] a nitrogen/phosphorus fertilizer to observe vegetative response to irrigation and fertilizatio[n].

During the winter of 1980-1981, we observed that mule deer were highly attracted to the irrigated a[nd] fertilized plots and were browsing heavily on big sagebrush plants within those plots. Untreated plots were mostly unbrowsed by deer. We also observed, during our fall inspection, significant vegetative response in the treated plots versus th[e] untreated plots. To quantify our observations, we repeated the irrigation and fertilization treatmen[t] in the spring of 1981 and took measurements to determine: big sagebrush response to the treatments, wintering mule deer use, and effects o[f] treatments on winter nutritive value of big sagebrush.

MATERIALS AND METHODS

Within a 160-ft radius, irrigated circle created b[y] a "big gun" sprinkler head applying about 220 gallons per minue, two treatment plots (270 by 270 ft [82.3 by 82.3 m]) were located. One plot received irrigation only; the other was irrigated and received 200 pounds of actual nitrogen per acr[e] and 100 pounds of actual phosphorus. Irrigation w[as] accomplished by applying 4.72 inches of mine water in an 18-hour period every 15 days. An untreated plot, the same size as the treated plots, was selected adjacent to the treatment plots and was comparable in aspect, slope, microrelief, vegetation, and soils. Big sagebrush plants were randomly selected for measurement in the three plots. Ten plants were selected in each plot. Th[e] 30 plants were tagged in the spring of 1981. Wire cages were placed around the plants after the growing season in October. During this time, eac[h] caged plant was paired with a nearby big sagebrus[h] plant of similar height, growth form, and leaf characteristics. These uncaged plants were used t[o] determine mule deer use and productivity. Caged plants were used to furnish the vegetative tissue[s] needed for nutritive analysis.

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On the uncaged plants, 20 or more leaders of :urrent annual growth per plant were measured after the end of the growing season, but prior to leer use. These measurements represented productivity (Welch and McArthur, this proceedings). After deer use, the remains of the same leaders were measured again to determine mule leer use. Use was expressed as a percent of current year's growth consumed.

At the time wintering mule deer were browsing on the plants, samples of current year's growth were removed from the caged plants. Samples were divided in half, placed in paper sacks, and frozen on site with dry ice. Vegetative samples were kept separate by individual plant and by treatment class. One half of the samples was used to determine monoterpenoid level and in vitro digestion; these were kept frozen until processed. Samples to be used for other chemical analyses were air-dried, ground in a Wiley mill, passed through a 1-mm sieve, and placed in airtight containers.

A steel, motorized mortar and pestle was precooled with liquid nitrogen before grinding the samples for monoterpenoid and in vitro digestion. Samples, one at a time, were placed in the mortar and another aliquot of liquid nitrogen was poured over the samples before grinding. After grinding, the samples were placed in plastic bottles fitted with airtight caps and stored at -35° F (-37° C).

Monoterpenoids were extracted in soxhlet extraction apparatus with absolute ethyl ether. For each sample, we placed 10 g of freshly ground tissue in a cellulose soxhlet extraction thimble. A fiberglass plug on top of the sample inside the thimble prevented spillover of tissue during the extraction process. Monoterpenoids were exhaustively extracted over a 6-hour period. The volume of the extract was reduced to about 30 ml by use of reduced pressure. We then added an internal standard carvone (2.5 g/ul) to each extract and absolute ethyl ether to bring the volume to 50 ml. Extracts were stored in airtight bottles at -35° F (-37° C) until chromatographic analyses.

We conducted chromatographic analyses with a 5830A Hewlett-Packard Flame Ionization, Recording Gas Chromatograph. Monoterpenoids were separated by use of 3-mm by 1.2-m stainless steel column packed with 10 percent carbo-wax 20M on 80/1000 Chromosorb WHP. Temperature programming was used to separate individual monoterpenoids (Welch and McArthur 1981). We identified monoterpenoids by comparing retention times with those of standards. Dry matter content of each sample was determined, and the concentration of individual monoterpenoids was expressed as a percentage of dry matter. Total monoterpenoids are the sum of individual monoterpenoids.

We used the in vitro digestion procedure as outlined by Pearson (1970), except 1.0 g of fresh tissue was placed in digestion tubes. Dry matter content was determined for all samples digested. Data were expressed as a percentage of digestible dry matter. Rumen inoculum was collected from a slaughterhouse steer fed alfalfa hay and barley (Welch and others 1983b).

For the air-dried samples, the following chemical measurements were made: oven-dry weight, ash, plant cell wall, hemicellulose, lignin, phosphorus, calcium, crude protein, starch, and sugar (Van Soest 1967; Association of Official Analytical Chemists 1980). Data were expressed on an oven dry-matter basis.

Data were statistically analyzed by random design analysis of variance and one-way heirarchical analysis of variance (Anderson and Bancroft 1952; Steel and Torrie 1960). Means were compared using Duncan's multiple range test ($\alpha = 0.05$).

RESULTS AND DISCUSSION

Productivity, as measured by length of current year's leader growth, was significantly greater for the irrigated-fertilized treatment than for the irrigated and unirrigated treatments. Average growth per leader for irrigated-fertilized was 10.7 cm, irrigated was 3.8 cm, and unirrigated was 2.3 cm. Irrigated-fertilized treatment increased plant growth by a factor of 2.8 over irrigated and 4.7 over unirrigated. What was surprising was that the irrigated treatment did not significantly increase plant growth over the unirrigated treatment. Apparently, soil fertility was a more limiting factor during the study period than soil moisture.

Analysis of variance detected significant ($\alpha = 0.063$) differential use by mule deer among treatments. There was a large intratreatment variation. The mean percentage of utilization for the irrigated-fertilized treatment was 56.1 percent (standard deviation ±19.1 percent). Utilization for irrigated and unirrigated treatments was 42.1 ± 14.2 percent and 29.4 ± 14.6 percent, respectively. Worthy of note is the high standard deviation associated with all treatments. Although sample size was too small to statistically detect significant differences among treatments at a lower or normal alpha ($\alpha = 0.05$) level, the trend favors heavier deer use on the irrigated-fertilized treatment.

It is important to note that while the difference in percentage utilization among treatments is not large, the difference in volume of materials consumed is quite large. Actual mean length of each current year's leader growth eaten is calculated by multiplying the mean leader length of a treatment by the percent utilization. Actual length consumed for the irrigated-fertilized treatment was 6.0 cm (10.7 cm x .561), for the irrigated treatment 1.6 cm (3.8 cm x .421), and for the unirrigated treatment .9 cm (2.3 cm x .394). The deer were consuming 3.8 times more leader length in the irrigated-fertilized plot than the irrigated plot and 6.7 times more than in the unirrigated plot. In the irrigated plot, deer consumed 1.8 times more leader length than in the unirrigated plot.

The results of the chemical analyses, tested statistically by a hierarchical analysis of variance and Duncan's multiple range test, disclosed significant differences among treatments, among plants within treatments, and between samples within plants. The unirrigated, irrigated, and

Table 1.--Chemical composition and digestibility of big sagebrush (Artemisia tridentata) growing on irrigated, irrigated-fertilized, and untreated plots on a Colorado oil shale mine site. Data expressed on a percentage dry matter basis. Both means and standard deviations are given

	Treatments			
	Unirrigated	Irrigated	Irrigated-fertilized	Mean
Plant cell wall	37.1 ± 3.1	35.3 ± 3.6	38.1 ± 3.1	36.8 ± 3.3
Hemicellulose	10.1 ± 2.4	9.8 ± 2.1	10.6 ± 2.5	10.1 ± 2.3
Cellulose	16.0 ± 1.9	15.2 ± 2.5	17.0 ± 2.5	16.7 ± 2.3
Lignin	10.7 ± 1.4	10.9 ± 1.9	10.5 ± 1.3	10.6 ± 1.6
Crude protein	11.8 ± 1.2[a]	12.4 ± 1.2[a]	15.8 ± 0.7[b]	13.4 ± 1.1
Starch	2.9 ± 0.5[a]	2.4 ± 0.3[b]	2.3 ± 0.5[b]	2.5 ± 0.4
Sugar	10.3 ± 2.4	9.7 ± 1.3	9.3 ± 2.2	9.8 ± 2.0
Ash	4.1 ± 0.5	4.5 ± 1.5	3.6 ± 0.4	4.1 ± 1.0
Phosphorus	0.076 ± 0.006[a]	0.087 ± 0.012[b]	0.088 ± 0.009[b]	0.084 ± 0.01
Calcium	0.241 ± 0.030[a]	0.253 ± 0.041[b]	0.221 ± 0.036[a]	0.238 ± 0.36
Digestibility	48.8 ± 3.2	50.8 ± 3.0	50.1 ± 2.9	49.9 ± 3.0

Treatment means sharing the same or no superscript are not significantly different (α= 0.05).

irrigated-fertilized treatments induced significant differences in crude protein (α= 0.001), starch (α= 0.01), phosphorus (α= 0.01), and calcium (α= 0.10) levels (table 1).

The irrigated-fertilized sagebrush plants were higher in protein and phosphorus and lower in starch than the unirrigated and the irrigated plants (table 1). Unirrigated (control) plants had the highest starch content and the lowest crude protein and phosphorus percentages. Irrigated plants were highest in calcium and in between for crude protein, starch, and phosphorus.

Individual plant variability was highly significant for all chemical constituents. The distribution of the variance components determined by hierarchical analysis of variance is shown in table 2 for protein, starch, calcium, and phosphorus-constituents significantly affected by treatment. Crude protein was the only component in which most of the variance was between treatments rather than between plants within a treatment. No replicate sagebrush samples were analyzed for crude protein, thus no information was obtained about within-sample variance.

Both starch and phosphorus had high within-treatment (between plants) variance; accounting for almost half of the total variance while within-treatment variance accounted for less than one-third and between-sample variance accounted for about one-fifth of the total variance. Calcium had a high between-sample variance, accounting for about one-half of the total variance. Only about one-tenth of the total variance for calcium was due to between-treatment variance while over one-third of the total variance was between plants within a treatment (table 2).

The nutritional results indicate that the irrigation-fertilization treatment caused crude protein levels to rise enough above the untreated sagebrush levels to play a major role in attracting mule deer to that plot. The higher phosphorus and lower starch also indicate that bi sagebrush, irrigated and fertilized, was probably in the vegetative growth stage longer compared to the more phenologically advanced control plants.

Energy-producing compounds, protein, and phosphor are nutrients commonly listed as being deficient

Table 2.--Distribution of variance components for chemical constituents significantly affected by nonirrigation, irrigation, or irrigation-fertilized big sagebrush (Artemisia tridentata) plants on a Colorado oil shale mine site

	Variance component			
Chemical constituent	Between treatments	Within treatments	Between samples[1]	Total variance
	%			
Protein	79.6	20.3	[2]--	100.0
Starch	31.5	46.6	21.9	100.0
Calcium	10.8	38.2	50.9	100.0
Phosphorus	30.5	48.9	20.5	100.0

[1]Variance is between replicated samples of the same plant.
[2]Protein analyses were not replicated on the same plant.

ble 3.--Monoterpenoid composition of big sagebrush (Artemisia tridentata) growing on irrigated, irrgated-fertilized, and nonirrigated plots on a Colorado oil shale mine site. Data expressed on a percent dry matter basis. Both means and standard deviations are given.

noterpenoid	Treatment			
	Unirrigated	Irrigated	Irrigated-fertilized	Means
-pinene	[1]0.03 ± 0.02[a]	0.09 ± 0.06[b]	0.09 ± 0.04[b]	0.07 ± 0.05
mphene	0.09 ± 0.06[a]	0.15 ± 0.07[b]	0.23 ± 0.14[c]	0.16 ± 0.11
8 Cineol	0.15 ± 0.10	0.21 ± 0.12	0.25 ± 0.18	0.20 ± 0.14
thujone	0.08 ± 0.04[a]	0.11 ± 0.07[b]	0.13 ± 0.05[b]	0.11 ± 0.06
mphor	0.55 ± 0.29[a]	0.81 ± 0.38[b]	1.22 ± 0.73[c]	0.86 ± 0.56
rpineol	0.05 ± 0.06	0.07 ± 0.07	0.04 ± 0.02	0.05 ± 0.05
nchyl alcohol	0.05 ± 0.06	0.07 ± 0.06	0.10 ± 0.09	0.07 ± 0.07
.36 (unknown)	0.16 ± 0.09[a]	0.23 ± 0.23[b]	0.39 ± 0.17[c]	0.26 ± 0.16
56 (unknown)	0.34 ± 0.55	0.17 ± 0.25	0.58 ± 0.77	0.36 ± 0.53
.70 (unknown)	0.28 ± 0.19	0.17 ± 0.10	0.17 ± 0.21	0.20 ± 0.17
tal	1.78[a]	2.08[b]	3.20[c]	

reatment means sharing the same or no superscript are not significantly different at the 5 percent level.
ımbers are retention times posted on the chromatogram.

ıble 4.--Distribution of variance components for monoterpenoids significantly affected by nonirrigation, irrigation, or irrigation-fertilization of big sagebrush (Artemisia tridentata) plants on a Colorado oil shale mine site

noterpenoid nstituent	Variance component		
	Between treatments	Within treatments	Total variance
	- - - - - - - - -	% - - - - - - - - -	
-pinene	22.4	77.7	100.0
mphene	14.8	85.2	100.0
thujone	19.1	80.9	100.0
mphor	26.7	74.4	100.0
36 (unknown)	32.6	67.4	100.0

e winter diet of mule deer and livestock (Dietz 55; Halls 1970; Nagy and Wallmo 1972). In vitro gestibility (a measurement of energy-producing mpounds) was at the 50 percent level needed for intenance (Ammann and others 1973). The in vitro gestibility found in this study compares closely the in vivo digestibility of big sagebrush ported by Dietz and others (1962) for th-central Colorado. Crude protein levels ranged om 11.8 to 15.8 percent, which is somewhat higher an that reported for big sagebrush in th-central Colorado by Dietz and others (1962), California by Bissell and others (1955), and in ah by Smith (1957). However, Welch and McArthur 979b) reported winter crude protein levels in 21 essions of big sagebrush ranged from 10.0 to 0 percent.

sed upon these substantial crude protein levels l the approximately 50 percent dry matter gestibility of big sagebrush, it is believed that gestible protein intake is above the maintenance uirements given by Welch and McArthur (1979a). n phosphorus levels ranged from 0.076 to 0.088 cent and are considerably below those recommended for maintenance by various authors (French and others 1955; Ullrey and others 1975; Welch 1983b). However, when big sagebrush is compared nutritionally with other range browse species in the West, it is generally rated good for wintering mule deer (Dietz and others 1962; Welch 1983a).

Analysis of variance detected significant differences both between treatments and within treatments for monoterpenoids (tables 3 and 4). Total monoterpenoids were significantly higher in vegetative tissue collected from big sagebrush plants under the irrigated-fertilized treatment (3.20 percent) than plants under irrigated (2.08 percent), and unirrigated (1.78 percent) treatment. As with browsing, there was considerable plant-to-plant variation. Of the ten individual monoterpenoids found, five were significantly affected by treatment. Irrigated-fertilized plants contained significantly higher levels of camphene, camphor, and 5.36 (unknown monoterpenoid) than plants not irrigated or irrigated only. Irrigated-fertilized and irrigated plants contained significantly higher levels of α-pinene and β-thujone than the unirrigated treatments. For these five monoterpenoids, the variability between treatments ranged from a low of 14.8 percent for camphene to a high of 32.6 for the unknown. Within-treatment (plant-to-plant) variance ranged from a low of 67.4 percent for the unknown to a high of 85.2 percent for camphene (table 4). The results of this study indicate that mule deer selected sagebrush material containing higher levels of monoterpenoids. The role monoterpenoids play in diet selection has been studied by a number of workers (Oh and others 1967; Sheehy 1975; Scholl and others 1977; Radwan and Crouch 1978; Connolly and others 1980; Schwartz and others 1980; Narjisse 1981; White and others 1982; Welch and others 1983a). Some of these have reported that monoterpenoids exert a negative influence on diet selection; others report no effect. The role monoterpenoids play in diet selection is confusing and far from resolved.

CONCLUSIONS AND SUMMARY

Water pumped during mine-dewatering efforts at the Cathedral Bluffs Oil Shale Mine was disposed of through a sprinkler irrigation system onto winter deer range. Mule deer use and chemical composition of big sagebrush was determined for plants receiving the mine-discharge water, mine discharge water along with a nitrogen-phosphorus fertilizer application, and plants in an unirrigated-unfertilized (control) plot.

The irrigated and fertilized sagebrush plants received moderate to heavy deer use during the mid- to late-winter period. Irrigated-only plants received light to moderate use, control plants received almost no use. The results of chemical analyses were tested statistically by analysis of variance using a hierarchical (nested) design. There were significant differences due to treatment for protein, starch, phosphorus, and calcium, but not for ash, plant cell walls, hemicellulose, cellulose, lignin, sugar, and in vitro digestibility. There were, however, significant differences within treatments indicating considerable variability among plants receiving the same treatment. Irrigated-fertilized plants were higher in protein and phosphorus, and lower in calcium and starch. Control plants were highest in starch and lowest in phosphorus and protein. Irrigated-only plants were highest in calcium and between the irrigated-fertilized and control plants in the levels of other nutrients.

The monoterpenoid content of big sagebrush was also determined. There was a significant difference in these oils due to treatment for α-pinene, camphene, β-thujone, camphor, and an unknown monoterpenoid. Within treatment, variance was high for all the monoterpenoids. The irrigated-fertilized plants contained the highest levels of α-pinene, camphene, β-thujone, camphor, and the unknown. The irrigated-only plants were in between in levels of these oils and the control plants contained the least, indicating that these essential oils did not negatively affect sagebrush utilization by mule deer.

Individual plant variability was much greater, in general, for the irrigated and irrigated-fertilized treatments than for the control. Uneven sprinkler and/or fertilizer application may have contributed to the wide variability among individual plants within treatments. Microsite differences, as well as the differential ability of plants to assimilate the fertilizer and mine water, may also have been a factor in the significant individual plant variability for the various chemical constituents.

Overall, our investigation indicated that big sagebrush was a good winter deer browse and that production, utilization, and nutritive value could be enhanced by irrigation and the addition of a nitrogen-phosphorus fertilizer.

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ECONOMIC CONSIDERATIONS IN MANAGEMENT OF SAGEBRUSH RANGES

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ABSTRACT: Economic factors give managers added information about the effects of various management strategies. In order to make meaningful economic analyses and comparisons of alternative management scenarios, accurate and sufficient physical information covering the fullest range of inputs and outputs possible must be available. Realistic alternatives should be developed and considered to assure that desired goals are being achieved and that scarce resources are being used in the most efficient manner. Deciding which factors are important, and realizing the true cost of taking actions can provide important comparisons before irreversible actions are taken. It is also important to study completed projects to see what impacts actually occurred so that future analyses can be more easily and accurately completed.

INTRODUCTION

Review of the literature and a considerable number of project analyses leads to the conclusion that some sagebrush rangelands can be successfully managed for profit or public benefit exceeding costs (Wagstaff 1983a). To be economically feasible, management must use good treatment techniques, reasonable cost control procedures, and good posttreatment management. With resources becoming scarce relative to demand, the need for efficient management of our sagebrush rangelands is increasing.

Rangelands are managed for the outputs in goods and services they are capable of providing. A good deal of thought is needed to identify and clearly state management goals for a specific unit of rangeland, this being the most crucial step in planning. Any conclusion about whether a project, treatment, or management action is good or bad must compare the results with the goals of management. Much of the difficulty in developing dependable and realistic management plans is due to unclear or contradictory goals (Alston 1972; Rensi 1979). Reasons for managing sagebrush rangelands are numerous and are often difficult to specify in measurable units.

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There are several economic principles and procedures of analysis which are useful when formulating treatment or management plans (Sneva and Britton 1982; Winward 1983). Every rangeland use has value, costs, and benefits (Randall 1979). A good deal of custom fitting of management and treatment procedures must be done on the basis of specific site characteristics. A given treatment can be applied to different subspecies of sagebrush at a uniform cost, but the productivity can vary quite widely. Only a portion of sagebrush rangelands have the physical characteristics needed for successful and profitable treatment to increase productivity.

Treatments to enhance productivity are done after specific decisions, such as method of treatment, time of treatment, species to be seeded, amount of rest, and the level and kind of posttreatment use, are made. Of all of these, the most important factor is setting management goals and followup actions to achieve those goals.

Using economic factors in decisions would lead to treatment area selection on the basis of the value of net production. The acres having the highest net would be treated first and then so on down the scale. Each acre should yield a ne benefit or it should not be treated. The net benefit or degree of economic efficiency associated with treatment of sagebrush ranges i affected most by posttreatment management of grazing (Nielson 1977).

BASIC ECONOMIC CONCEPTS

The concept of benefits and costs is very important. Benefits are the desirable impacts of a project or management action; however, wha is considered desirable depends upon the goals of the land manager. For example, a complete brush kill may be perceived as highly desirable for livestock production by a private owner while game managers may feel this would be undesirable.

Costs are negative impacts that can take the form of money costs, resource obligation, opportunities foregone, or damages. The conce of costs is also subject to the goals and valu of the land manager. It is important to identify and categorize all impacts of an acti so benefits and costs can be compared.

Opportunity cost is the value of the best alternative foregone. If removal of brush

recludes wildlife use of an area, then the net enefits for wildlife not realized become an pportunity cost.

arginality is a concept that holds that each ivisible part of a project should be looked at eparately. Applying this concept to rangelands eans we should look at an area on the basis of oil type, vegetation, and other indicators of roductive potential. When real differences ccur in productivity, net benefits will also iffer. Treatment costs are often the same egardless of the difference in soil or subspecies f sagebrush. Only those units where benefits xceed costs can be treated or managed conomically.

ilues

iluing outputs is a very important concept ecause feasibility depends directly on those ilues. Were all outputs traded in markets, a ice or unit value could be obtained rather isily. However, many rangeland uses and outputs e of the nonmarket type and setting values is iprecise and difficult. Many things, such as ldlife, scenery, and enjoyment of open spaces, on which people place a good deal of value, are nmarket in nature. Problems arise when market d nonmarket outputs are included in an analysis d trade-offs are indicated. Ignoring nonmarket it values does not make the problem easier oung 1979; Bartlett 1982).

istribution

oblems can arise when one group gains benefits d another pays the costs (Wagstaff 1983b). Such oblems occur frequently with wildlife where the blic gains benefits from wildlife and the ivate landowner may suffer loss of resources to ldlife use.

scounting

e other economic concept needs to be mentioned give a general base for analysis. Discounting used to make future benefits and costs mparable to present-day values (Nielsen 1977; DA 1982). Essentially, discounting is applying expected rate of interest and reducing future lue by this amount. The concept rests on the ct that future incomes or expenses are not lued as highly as those occurring at the esent.

ure expenses can be met by deposit of an amount er than the cost with the remainder being erest earned. Likewise a future benefit is luced in value to account for the opportunity t of capital (interest which could be earned) a risk factor.

NOMIC FACTORS AS DECISION CRITERIA

ry use connected with rangelands has value, ts, and benefits (Randall 1979). Funding is limiting, however, and many other uses of these funds can be made, so proposed expenditures for treatment or improvement of sagebrush rangelands must be compared to alternative uses (Kerr and Dooley 1982). Private landowners are faced with a dual problem. Borrowing money is expensive, with double-digit interest rates common. Also, capital or equity funds can be invested in the money markets or other low-risk investments and command 10 to 12 percent interest rates. These rates are high when compared to the average rate of return common in ranching enterprises. Most resource agency budgets have been declining, and the short-term outlook is for more reductions. This means a closer look must be taken at the costs and benefits associated with sagebrush rangeland treatment projects and management activities.

ECONOMIC DECISION CRITERIA

There are many criteria that can be used in making rangeland management decisions. Economics is usually just one factor in a decision and can be of major or minor importance. More attention is now being paid to economic factors of public projects due to the high price of capital and increased competition for tax dollars among public programs.

As pointed out by Workman (1981), the use of different criteria may change decisions. A few basic economic measures that are widely used are:

Net Present Worth.--The present value of future benefits minus all costs. The level of net benefits depends on the unit values used for costs and benefits, the time frame, and mostly, the rate of discount.

Rate of Return.--Is the annual rate of return on the investment received as net benefits.

Benefit-Cost Ratio.--The ratio of total benefits/total costs. All benefits and costs should be compared on an equal time frame so discounting is needed. Generally, present values of benefits and costs are used although other techniques can yield identical results.

Payout or Break-Even Period.--The length of time it would take to return the original investment. Only benefits above operation and maintenance costs can be applied to investment recovery. If borrowed funds were used, this would be the period of time required to repay the loan.

Cash Flow Analysis.--Amount of cash expected to be received or paid during a given time interval.

Distribution Analysis.--The incidence of benefits and costs is often quite important. Who pays and who gains should be set forth in an analysis so that questions of equity among individuals or groups can be addressed (Keith 1983; Obermiller 1983). There has been increasing resistance to programs which benefit few persons.

A couple of major points concerning physical characteristics and related economic principles need to be made. Treatment costs and responses are often viewed as linear functions across large changes in project size.

A more reasonable cost function would follow a more classic pattern: reducing costs to a certain size, then increasing cost per unit treated. Production functions could be viewed as essentially linear as long as the same sagebrush subspecies is being treated and the soil, climate, slope, aspect, and other physical features remain constant. The temptation is to treat large areas, thereby reducing unit costs as much as possible. However, this may not be as efficient as treating only the most productive acres (Bartlett and others 1974; D'Aquino 1974). Treatment costs per unit of land may be higher by doing selected areas, but the net difference between costs and benefits can be greater because of the higher production per unit treated.

VALUE OF ADEQUATE PHYSICAL DATA

Without accurate estimates of the physical parameters, economic analysis is of little value. Any errors in the estimates of inputs and outputs will be magnified in an analysis. There is a tendency among analysts to accept estimates by range conservationists as completely accurate. As Clary (1983) pointed out, the need for sampling points to obtain statistically sound estimates is great. In the absence of budgets or manpower to get such estimates, we tend to rely on small sample estimates from a number of projects over a diverse area and time interval. Perhaps analysis should be done with bands of confidence rather than merely giving single point estimates.

Two factors loom large in estimates of production. Climatic variation can dramatically alter production (Sneva and Britton 1983), and management can offset almost all other factors.

The best estimates of input and output data should be used. Extrapolation of data can be very misleading unless adjustments for site differences are made. Disregard of the physical factors can lead to improper treatment or management. This then leads to projects which do not perform well and waste money (Nielsen 1977). Also, costly mistakes can be made that set ecological processes in action that are very difficult and expensive to change.

Whenever possible, numerous projects in close proximity to the proposed area should be studied to determine their degree of success and reasons for success or failure. Close attention needs to be given to basic physical data such as soil, climate, sagebrush subspecies, understory, adapted species for introduction, and associated wildlife species. Disregard for these or other significant factors can cause project failure that can be very expensive both economically and environmentally.

To be most helpful, physical parameters must be of two general types. First, the basic input-output relationships relevant to the site need to be identified. What output levels can be achieved for what level of inputs? A general form of this function is shown in figure 1 where one output from one input is graphically portrayed. Such a physical function can be converted to an economic one by pricing the output and input.

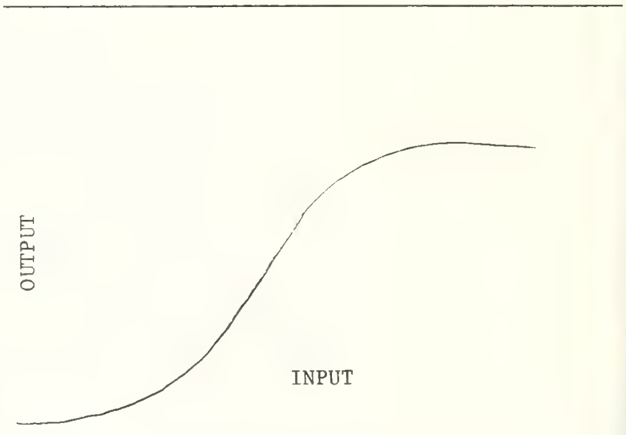

Figure 1.--Conceptual input-output curve.

Figure 2 may show, for example, how forage can be used by two species of grazing animals. At some point of use there will be competition for forage. The more complete the dietary overlap between animal species, the greater competition will be, if other factors are not limiting. For example, a small number of elk may not reduce forage available for cattle on a range where lar numbers would. Figure 2 shows an output-output transformation function. It is so called becaus it shows the amount of each (or both) species th can be produced using a set amount of forage on range area.

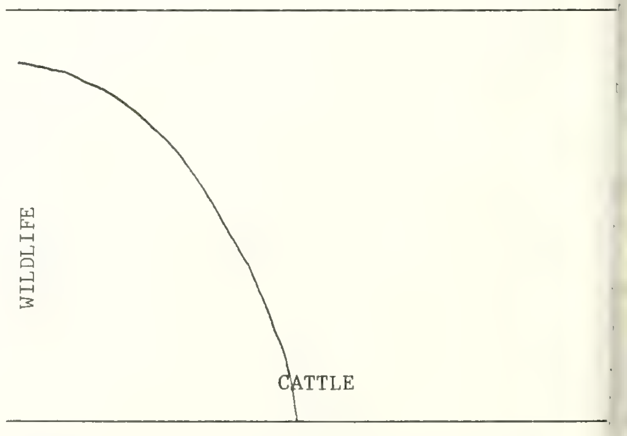

Figure 2.--Output-output or transformation function.

f the value of wildlife and livestock is known, he best or most profitable combination can be etermined. The problem is that input-output and radeoff relationships usually are not well efined, estimates are often not as accurate as hey should be, and values for wildlife are not eadily determined. Therefore, decisions are made n scanty information. More information about hese basic relationships could lead to less ostly methods of producing forage.

AKING AN ECONOMIC ANALYSIS

ie major step in making an economic analysis is eveloping realistic alternatives. There may ppear to be only one option, but a closer look sually reveals possible changes. Alternatives iould be legally, administratively, and echnically feasible. The physical relationships f outputs and inputs for each alternative must be etermined and quantified. Selection criteria, als, or purposes for all alternatives should be ecified. This will allow comparison and ranking f the alternatives, and selection of the best otion.

ojects and alternatives should be of the size, ale, or intensity that would best meet inagement goals. If economic criteria are given, ight increments or units of inputs should be ded until the additional costs of adding other its are just equal to the benefits expected arginality concept).

ce benefits and costs are determined by amount d time of occurrence, the process of discounting ll adjust them for time differences. The last ep is determining the net benefit level for each the alternatives and making any other economic nking tests.

rlew National Grasslands

e data in table 1 are from analyses of velopment projects on the Curlew National asslands in southern Idaho. On the Grasslands, riodic treatment of sagebrush is needed to keep azing capacities high. There are three main ys of reducing sagebrush once it has dominated a te long enough to reduce understory forage ants beyond a point where natural recovery would be accomplished in a reasonable time. These methods have different costs. The chaining method has a different potential production level. The increased production is valued by determining a value for livestock forage.

In table 1, two values for grazing are shown to reflect the local practice of making winter use of crested wheatgrass seedings. As the data show, winter grazing is considerably more valuable since it substitutes for hay while summer grazing substitutes for other grazing.

The results of summarized analyses show positive percent values less costs except for summer grazing with chaining and broadcasting seed. An expanded analysis summary could include other uses, such as recreation or wildlife, and other methods. The most economic alternative presented in table 1 is burning and drilling seed. Winter use with this method shows the best return per dollar of investment.

DISCUSSION

It is rare that project plans are compared to results. In order to determine which estimates were good, physical success and productivity should be monitored. Many times, post-project grazing use is delayed due to poor treatment techniques or adverse weather. Such delays have a significant financial impact on permittees and project economics.

By looking at completed projects, land managers should be able to make better estimates. Also, probability estimates can be introduced to give confidence bands around the estimated impacts of a new project. Building a data base and confidence in analysis techniques is time consuming and difficult. Much better estimates are needed to significantly upgrade analyses. If sagebrush rangeland projects are to compete successfully for funds, they must be presented in the best possible light. This means counting all benefits and producing reliable and realistic analyses. Also, treatment of all areas in a uniform manner, whether the output is to be used or not, could be eliminated. More selectivity is necessary if rangeland projects are to be competitive with projects of other kinds.

ble 1.--Summary of analysis of sagebrush range improvement, Curlew National Grasslands[1]

provement method	AUM/acre			Value of increase/acre		Discounted value		Discounted value-costs	
	Without treatment	With treatment	Increase	Summer	Winter	Summer	Winter	Summer	Winter
ow and drill	0.1	0.5	0.4	$2.80	$6.00	$24.89	$74.77	$4.89	$44.77
ain and broadcast	.1	.3	.2	1.40	3.00	17.45	37.39	-2.55	17.39
rn and drill	.1	.5	.4	2.80	6.00	34.89	74.77	24.89	64.77

ata on file at Shrub Sciences Laboratory, Intermountain Research Station, Forest Service, U.S. Department f Agriculture, Provo, UT.

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Section 4. Animal Relationships

PREY POPULATIONS IN RELATION TO ARTEMISIA VEGETATION TYPES IN SOUTHWESTERN IDAHO

Nicholas C. Nydegger and Graham W. Smith

ABSTRACT: Densities of Townsend ground squirrels and black-tailed jack rabbits are reported for *Artemisia* and related vegetation types in the Snake River Birds of Prey Study Area. The presence of shrubs is critical to black-tailed jack rabbits and may benefit Townsend ground squirrels. Habitat maintenance is essential to the preservation of the breeding population of birds of prey which utilize black-tailed jack rabbits and Townsend ground squirrels as primary prey species.

INTRODUCTION

Habitat-specific abundances of raptor prey species were investigated within the Snake River Birds of Prey Study Area (BPSA) to aid in the evaluation of critical habitat, to determine the response of prey species to habitat alteration, and to examine predator-prey interrelationships. The BPSA has one of the densest nesting populations of raptors in the world (USDI 1979). More than 600 pairs representing 15 species nest in the area annually.

One of the most important factors contributing to the diversity and density of raptors in the BPSA is the abundance of prey species. Diversity in vegetation or habitat types allows a variety of prey species to exist. Prey species include: lagomorphs, rodents, a variety of other mammals, reptiles, amphibians, insects, other arthropods, and avian prey.

In this paper we address the two most important prey species in the BPSA: the Townsend ground squirrel (*Spermophilus townsendii*) and the black-tailed jack rabbit (*Lepus californicus*). The U.S. Department of the Interior, Bureau of Land Management (BLM) Birds of Prey Research Project has shown a significant correlation between prairie falcon (*Falco mexicanus*) productivity and Townsend ground squirrel abundance. They have also shown a significant correlation between golden eagle (*Aquila chrysaetos*) productivity and black-tailed jack rabbit abundance (USDI 1979). Plant names follow Welsh and others (1981).

STUDY AREA

The BPSA encompasses about 837,000 acres (339 000 ha) in southwestern Idaho along an 81 mi (130 km) stretch of the Snake River. Canyon walls, numerous buttes, and side canyons provide ideal nesting sites for raptors.

The area ranges from about 2,300 to 3,500 ft (700-1 067 m) in elevation. The topography is flat to rolling with scattered volcanic cones and buttes. Precipitation ranges from 7 to 10 inches (18 to 25 cm) per year with the majority falling from November through March. Vegetation ranges from sagebrush/grassland to salt desert shrub (Sharp and Sanders 1978).

VEGETATION

In 1977 and 1978, the vegetation within the BPSA was mapped. Homogeneous stands of vegetation were identified from 1:31680 scale color aerial photographs. Each vegetation stand was delineated on 7.5' USGS topographic maps. Only stands greater than 40 acres (16. ha) were mapped. In 1979, all boundaries between vegetation stands were verified on the ground and refined. The vegetation in each stand was sampled along a 1,312-ft (400-m) transect line. At least one transect was sampled in each vegetation stand. More than one transect was sampled in some large stands. A total of 40 canopy cover estimates, using the technique of Daubenmire (1959), were systematically taken on each transect line. Fifteen 1/300-acre (13.5-m^2) density plots were also systematically sampled on each transect line to assess the density and height of shrubs (Asherin 1973).

Habitat or cover types were identified primarily on the basis of dominant shrub species. We address 10 cover types: big sagebrush (*Artemisia tridentata* spp. *wyomingensis*); big sagebrush/winterfat (*Ceratoides lanata*) mosaics; big sagebrush/shadscale (*Atriplex confertifolia*) mix; big sagebrush/rabbitbrush (*Chrysothamnus* sp.);

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winterfat, shadscale; shadscale/winterfat mix; rabbitbrush; black greasewood (Sarcobatus vermiculatus); and a grass type. An examination of the mean percentage plant cover (table 1) and the mean shrub density (table 2) for each cover type shows that each type was named for the dominant shrub species present with the exception of bud sagebrush (Artemisia spinescens). Bud sagebrush occurred as a codominant with shadscale throughout the study area and was ignored in naming types. Tables 1 and 2 also reveal that each cover type is indeed a unique plant community.

TOWNSEND GROUND SQUIRRELS

Methods

Townsend ground squirrels were live-trapped annually on five, 2.47-acre (1-ha) study sites from 1975 to 1979. Site 1 was located within a big sagebrush stand, site 2 in a heavily overgrazed stand of winterfat, site 3 in a healthy stand of winterfat, site 4 in an annual grassland (the result of a 1974 range fire), and site 5 in a big sagebrush/winterfat mosaic. Twice weekly from February to June of

able 1.--Mean percent canopy cover by species for cover types in the Snake River Birds of Prey Study Area

over type	Big sagebrush	Big sagebrush/ winterfat	Big sagebrush/ shadscale	Big sagebrush/ rabbitbrush	Winterfat
rtemisia spinescens	0.3	0.2	2.9	0.2	1.1
rtemisia tridentata	11.8	7.2	3.6	7.4	
triplex confertifolia			6.0	.5	
rayia spinosa	.8	1.4	1.2	.6	.4
eratoides lanata		11.3	.2	.3	22.2
hrysothamnus sp.	T[1]			2.9	
arcobatus vermiculatus		.3			
romus tectorum	6.8	3.4	5.3	6.4	1.9
ulpia octoflora	1.8	1.7		.1	1.9
ryzopsis hymenoides	.1			.7	
oa secunda	2.9	5.7	1.3	1.0	4.2
itanion hystrix	1.6	1.4	1.1	.7	.8
escurainia pinnata	.4	.9	.2	.1	.8
alogeton glomeratus	T		.3	T	
alsola iberica	.6	.1	1.2	1.4	.1
isymbrium altissimum	.9	.1	.4	1.4	
are ground	74.2	69.8	78.3	77.1	67.4

able 1.--Continued

over type	Shadscale	Shadscale/ winterfat	Rabbitbrush	Greasewood	Grass
temisia spinescens	3.7	3.8	0.1	0.8	T
temisia tridentata				1.8	.1
riplex confertifolia	6.7	6.4		1.0	
ayia spinosa	.6	.4		.7	
ratoides lanata	T	9.0			
rysothamnus sp.	.2		8.0	.6	.1
rcobatus vermiculatus				8.0	
omus tectorum	3.4	3.1	6.8	6.7	11.4
lpia octoflora			.2	.2	1.0
yzopsis hymenoides	.1		.1	.2	.2
a secunda	.8	.2	5.4	.5	2.2
tanion hystrix	.8	1.2	.2	.4	.7
scurainia pinnata	.3	.4	.2	.6	.9
logeton glomeratus	.2	.1		.9	.1
lsola iberica	.6	.5	3.0	1.5	3.1
symbrium altissimum	.4		3.8	.6	3.5
re ground	80.8	75.9	69.6	74.7	71.2

[1] T=trace (1979 data)

Table 2.--Mean dominant shrub density by cover type in the Snake River Birds of Prey Area

Cover type	Species	Mean density	SF[1]	Height	SE
		N/ha		cm	
Big sagebrush	*Artemisia tridentata*	5,565.6	354.8	49.1	1.1
Big sagebrush/ winterfat	*Artemisia tridentata*	3,579.1	571.1	51.1	1.9
	Ceratoides lanata	20,145.4	2,500.4	16.5	.8
Big sagebrush/ shadscale	*Artemisia tridentata*	1,074.4	293.3	44.9	2.5
	Atriplex confertifolia	3,019.9	722.1	27.6	1.3
	Artemisia spinescens	2,645.6	727.0	15.3	.8
Big sagebrush/ rabbitbrush	*Artemisia tridentata*	2,744.2	426.4	54.5	2.7
	Chrysothamnus sp.	1,199.2	240.2	36.1	2.0
Winterfat	*Ceratoides lanata*	34,518.4	3,790.5	18.5	1.2
Shadscale	*Atriplex confertifolia*	4,171.3	600.2	25.9	1.1
	Artemisia spinescens	3,664.1	623.7	16.2	.8
Shadscale/ winterfat	*Atriplex confertifolia*	3,132.1	780.6	29.4	1.6
	Artemisia spinescens	3,354.2	1,462.7	13.8	.6
	Ceratoides lanata	13,559.5	3,979.5	23.0	.8
Rabbitbrush	*Chrysothamnus* sp.	5,596.0	1,729.1	35.27	2.2
Greasewood	*Sarcobatus vermiculatus*	1,258.8	184.9	71.8	3.6
Grass	None				

[1] Standard error.

each year twenty, 16-by 5-by 5-inch (40-by 13-by 13-cm) live traps were set randomly about specific locations on each grid, baited with apple, and checked three times daily. Squirrels were permanently marked by toe clipping. April population estimates on each grid were obtained using CAPTURE, a computer program for analysis of capture-recapture data (Otis and others 1978).

Due to the time involved in using the trapping technique, it was not possible to live-trap all cover types. To ascertain ground squirrel abundance in all cover types another technique was employed. In 1978 and 1979, ground squirrel burrows were counted on approximately 350 systematically located transects. Each hole-count transect was 17 ft 10 inches (5 m) wide and 1,312 ft (400 m) in length. All active ground squirrel burrows within this strip were tallied by an observer traversing the center line of the transect. Data were stratified by cover type, and the mean number of holes per cover type was calculated. Hole-count transects were also established on each of the five, 1-ha, trapping sites. Regression analysis of the average density (1975-79) and the hole counts on each trapping site showed that ground squirrel density and the number of burrows present were significantly correlated (r=0.94, $\underline{P}$=0.002, fig. 1). Eighty-nine percent of the variation in ground squirrel density was explained by burrow density. By substituting the average hole count for each cover type into the regression

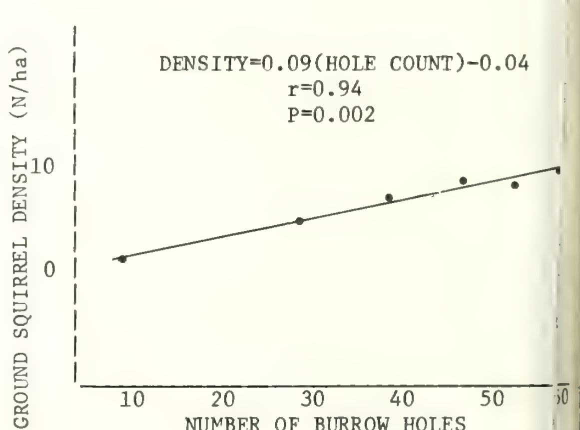

Figure 1.--Townsend ground squirrel hole cour regression, trapping grid density on burrow hole counts, Snake River Birds of Prey Study Area.

equation, densities were determined for each cover type (table 3).

Results and Discussion

An examination of ground squirrel densities y cover type within the BPSA (table 3) reveal that the big sagebrush/winterfat, winterfat and grassland types support the largest populations of ground squirrels. These thr vegetation types are probably most importan to the maintenance of this prey base; however, he wide distribution of ground squirrels in th

ther cover types lends importance to them lso. Ground squirrel abundance can be related o soils as well as vegetation. The deep soils ssociated with the big sagebrush and winterfat ommunities are important to this burrowing odent.

able 3.--Townsend ground squirrel density by cover type, Snake River Birds of Prey Study Area

over type	Mean number of burrows	Predicted[1] density	SE[2]
		N/ha	
ig sagebrush	19.2	1.72	.84
ig sagebrush/ winterfat	31.6	2.86	.72
ig sagebrush/ rabbitbrush	19.0	1.70	.84
ig sagebrush/ shadscale	20.7	2.96	.72
interfat	32.7	1.45	.88
hadscale	16.2	1.48	.87
abbitbrush	18.2	1.63	.85
reasewood	Insufficient data		
rass	28.1	2.54	.75

Based on regression of 1975-79 mean trapping grid density on trapping grid hole counts.
Standard error.

round squirrels eat green plant material, articularly grasses. Important species are andberg's bluegrass (Poa sandbergii), eatgrass (Bromus tectorum), a variety of rbs, and some shrubs (Johnson 1977; Smith and hnson in press). The shrub communities ntaining native perennial grasses and forbs well as annuals probably support more stable pulations in the long term as they are not as everely impacted by annual climatic uctuations as are annual grasslands. They so offer more diversity in microhabitat than e monoculture of annual grasslands, thus een vegetation is available for a longer riod of time.

ACK-TAILED JACK RABBITS

thods

ack-tailed jack rabbits were surveyed nually from 1979 to 1981 on 11 spotlighting ansects (Flinders and Hansen 1973; Smith and degger in press) running through the major getation types within the Study Area. ansects varied from 1 to 32.8 mi (1.6 to 53 km) in length. Transects were surveyed each year beginning in mid-May. Three replicates of each route were completed by early June. Surveys were begun about 10 p.m. when it was dark and were completed before 5 a.m. when it began to get light. One technician drove a pickup truck at 5 to 10 m/h (average 7 m/h, 11 km/h) while another technician spotlighted from the truck bed. Approximately 350 mi (560 km) of transect were surveyed each year. Data were stratified by cover type and analyzed using TRANSECT (Burnham and others 1980), a computer program for analysis of line transect data.

Results and Discussion

Black-tailed jack rabbits were most abundant in the big sagebrush and black greasewood cover types (table 4) and occurred somewhat equally in those other types with some species of tall shrub present. Shrubs provide the cover necessary to protect the jack rabbit, which does not burrow, from predators and environmental extremes. Shrubs also provide food in the winter months. Donoho (1972) found that black-tailed jack rabbit densities were proportional to shrub density in Colorado. Those cover types listed as insufficient line length (table 4) are cover types without adequate transect length in any year. The winterfat and grass cover types (noted as insufficient data in table 4), both had in excess of 20 mi (32 km) of transect length each year. Few rabbits were seen in these types

Table 4.--Mean black-tailed jack rabbit density 1979-81 from spotlight line-transects, Snake River Birds of Prey Study Area

Cover Type	Density[1]	SE[2]
	N/ha	
Big sagebrush	0.81	0.06
Big sagebrush/ winterfat	.24	.07
Big sagebrush/ rabbitbrush	Insufficient line length	
Big sagebrush/ shadscale	.43	.11
Winterfat	Insufficient data	
Shadscale	.42	.08
Shadscale/winterfat	.39	.09
Rabbitbrush	Insufficient line length	
Greasewood	.92	.18
Grass	Insufficient data	

1 Calculated using program TRANSECT (Burnham and others 1980).
2 Standard error.

especially within large homogeneous stands away from ecotones. In effect, the winterfat and grassland types do not support black-tailed jack rabbit populations within our study area.

HABITAT ALTERATION

Habitat alteration occurs from three sources within the area; fire, brush removal to enhance forage production and conversion to agriculture. With the withdrawal of the BPSA in 1980 agricultural encroachment has been halted. Conversion of native range to agriculture is detrimental to both black-tailed jack rabbit and Townsend ground squirrel populations through loss of habitat, disturbance, and control programs. Brush removal has not been utilized to any magnitude within the study area, but depending on the technique used, its effects are similar to fire.

The primary cause of habitat alteration within the study area is wildfire. Huge blocks of native rangeland burn each year. Eighty thousand acres (32 400 ha) burned in 1983, 20,000 acres (8 100 ha) in 1982, and 78,000 acres (31 600 ha) in 1981 (USDI unpublished fire records). Along with loss of shrubs, large blocks of land are being invaded by exotic annuals, primarily cheatgrass. These areas then become susceptible to repeated burning (Stewart and Hull 1949). As shrubs are eliminated, these areas become unsuitable to black-tailed jack rabbits and the Townsend ground squirrel becomes more vulnerable to both predation and annual climatic fluctuations. Overall, we see reduced diversity in prey species, reduction in habitat, and ultimately reduced prey productivity within these areas.

The continued existence of the breeding population of birds of prey in this area is dependent on the maintenance of prey populations and ultimately the maintenance of a shrub and grassland mosaic.

We need increased knowledge of habitat use by both predator and prey species to more closely examine the impacts of habitat alteration and rehabilitation efforts. Because the majority of current rehabilitation efforts are targeted at domestic grazing we need to develop rehabilitation techniques that maximize benefits to both wildlife and domestic species.

ACKNOWLEDGEMENTS

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SAGE GROUSE-SAGEBRUSH RELATIONSHIPS: A REVIEW

Jay A. Roberson

ABSTRACT: This paper was written to synthesize and suggest management application of sage grouse-big sagebrush research. In the life of sage grouse, big sagebrush and other sagebrush species are most critical for food and cover during winter and breeding-nesting periods. The strutting ground is the hub of year-round activity, but structural components of big sagebrush used for nesting, the proximity or interspersion of nesting, brooding, and male feeding-loafing areas to the strutting ground, and natal fidelity appear to be more important than structural characteristics of the strutting ground itself. Suitable male sage grouse feeding-loafing sites within 0.6 mile (1 km) of the strutting ground are critical for optimum use of the strutting ground. Males use big sagebrush plants that are taller and have greater canopy cover than random plants on the site. Loss of feeding-loafing sites around strutting grounds has resulted in population declines. Sage grouse hens nest almost exclusively under big sagebrush plants that are taller with greater canopy cover than the average.

Big sagebrush control should not be conducted on sage grouse sites where big sagebrush plants are less than 12 inches (30 to 48 cm) tall with less than 20 percent canopy cover. Also big sagebrush control should not be conducted on big sagebrush plants 7 to 30 inches (17.78 to 76.2 cm) tall with 20 to 40 percent canopy cover within 2 mi (4.8 km) of strutting grounds. Tall, dense, robust clumps of big sagebrush at the head of shallow draws and hollows should be protected for nesting habitat. Water developments should be protected, maintained, or constructed within 1 mi (1.6 km) of nesting habitats in zeric zones (less than 10 inches [25 cm] of rainfall).

INTRODUCTION

This report is a survey of literature and, based on that review, some recommendations for research and management. My purpose is to identify critical sage grouse-big sagebrush relationships, recommend management practices to protect habitats, and suggest areas of needed big sagebrush research.

No other North American game bird is so highly specialized and so inextricably dependent upon one plant species as sage grouse (Centrocercus urophasianus) is on big sagebrush (Artemisia tridentata) and its near relatives. Sage grouse has a near obligate relationship with big sagebrush and its close relatives of the subgenus Tridentatae of Artemisia. There is no evidence that sage grouse can adapt to changing vegetation resulting from human land use practices. Schoenberg (1982, p. 76) states that sage grouse select winter, breeding, nesting, and brood-rearing habitats on the basis of suitable structure and probably big sagebrush subspecies composition. It cannot be assumed that grouse will move elsewhere and maintain the same populations present before disturbance of preferred habitats.

A great deal of similarity exists between Beetle's (1960) map of the distribution of big sagebrush and Braun's (1985) unpublished map of sage grouse distribution. Sagebrush is used as food or cover in every season of the year (Girard 1937; Griner 1939; Patterson 1952; Klebenow 1969; Peterson 1970; Wallestad 1971; Eng and Schladweiler 1972).

Big sagebrush habitat types are declining in size. Estimates of big sagebrush lands altered to improve grass productivity range from 4.9 to 24.7 million acres (2 to 10 million ha) (Schneegas 1967; Braun and others 1976) from an original range of 144.9 to 269.9 million acres (58.7 to 109.3 million ha) (Beetle 1960; Sturges 1973).

Eradication of large areas of big sagebrush has been found to be detrimental to sage grouse (Autenrieth and others 1977). Sage grouse harvests in most states and provinces have declined in the last 10 to 15 years. These trends indicate actual population declines since harvest regulations have not changed appreciably and hunter effort has increased (Donoho and Roberson 1985).

Sage grouse are a unique wildlife resource with historical, scientific, and esthetic value deserving careful consideration. They are the largest North American grouse with some adult males reaching 7 lb (3.2 kg). Their reproduction rates are among the lowest of any upland game bird due to their relatively high

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rate of nest desertion, especially among yearling hens, delayed age of first breeding, relatively small clutch sizes, and high chick mortality. They differ from other tetraonids in not having a muscular grinding gizzard. Thus, they are generally restricted to soft-tissue foods. Before 1940, and the establishment of ring-necked pheasant (Phasianus colchicus), sage grouse was the most popular and heavily hunted game bird in the western states.

Although numbers are declining, sage grouse remain an important recreational resource. During 1980, an estimated 110,000 sage grouse hunters in western North America harvested 245,000 birds (Donoho and Roberson 1985). Based on a 1972 estimate of $19.45 per hunter trip in Idaho (Autenrieth 1981), sage grouse hunting in the West generates over $2 million to local economies. Additional money is spent on nonconsumptive use.

Conflicts between sage grouse and livestock do not arise from direct competition between the animals, but from competition between their food resources--big sagebrush versus grass. It has been stated but is difficult to prove that big sagebrush ties up soil moisture and nutrients otherwise available to perennial grasses (Sturges 1975). It has been just as difficult to prove sage grouse population declines result from big sagebrush eradication. Obviously, grass production as measured by pounds of air-dry matter per unit area can be doubled or tripled by removal of big sagebrush; however, from an ecological point of view, the grass increase is only temporary and big sagebrush reinvades. It is obviously part of the climax vegetation. Apparently big sagebrush adds species diversity and therefore ecosystem stability, improves transfer efficiency, and leads to a biotic community better buffered against disease and weather (Daubermire 1970; McArthur and Plummer 1978). It also reduces soil erosion by interrupting precipitation and provides for deeper snow accumulation. Daubenmire (1970) raised concerns about attempts to eradicate sagebrush which were again raised by Autenrieth (1981). These concerns were:

1. "There is little evidence to indicate the extent to which the desired grass increase (measured shortly after shrub eradication) is maintained. . . ."

2. "The protection afforded many grass plants by dense clumps of shrubs is the sole reason why any perennial grass remains on much of the depleted ranges. Artemisia elimination opens the way to complete destruction of perennial grass by overuse."

3. "Studies in Washington (Daubenmire 1969) have shown that for more than 4 months in the summer Artemisia tridentata uses only what water has percolated through the soil profile below the reach of grass roots. . . . The question should be raised: to what extent does the removal of this shrub allow some minerals to migrate permanently below the reach of grass roots. . . ."

4. "Removing Artemisia eliminates certain elements of the avifauna. While rearing their young these birds make a heavy drain on insect populations. Increased insects may damage the residual grass."

5. "When Artemisia is removed by herbicidal sprays, certain perennial broadleaved forbs are heavily damaged or eliminated (Hurd 1955, Blaisdell and Mueggler 1956, Mueggler and Blaisdell 1958, Anon. 1968). The loss is generally ignored on the tacit assumption that the unharmed grass, which supplies nearly all the domestic animals' food and which may produce more because competition is lessened, is the only component of economic significance. However, depending on the kind of vegetation and type of animals involved, spray removal of Artemisia may entirely destroy many desirable plant species and allow their replacement by inferior species and forage production may be seriously reduced for a period of several years (Blaisdell and Mueggler 1956). In western Colorado herbicides reduced forb production by 95%, yet these forbs contained more protein than the best of the forage grasses (Anon. 1968). . . ."

6. "In most areas Artemisia promotes the uniform accumulation of snow and delays its melting; both are desirable from the standpoint of range management (Hutchinson 1965). Several of the consequences of Artemisia removal enumerated above involve an important ecologic principle. The more diversified the biota of an area, the more completely the environmental resources are being used, and the better the community is buffered against disease and weather hazards. Simplification of shrub-steppe vegetation by removing a major component that contributes a distinctive life form an phenology, and is necessary for other species to remain in the community, cannot fail to have serious consequences. If herbicides are used to remove Artemisia, other species are also eliminated. Rather than focus interest on just the quantity of grass available and acceptable to one class of domestic animal, those points should be studied broadly."

I agree with Autenrieth and others (1977) who state that simplification of shrub-steppe vegetation by removing a major life form and phenology in order for other species to remain in the community cannot help but have serious consequences. I do not deny that removal of bi sagebrush significantly reduces soil moisture loss (Sturges 1973), increases dry matter production by forbs that remain, and makes gras more readily available to livestock (Daubenmire 1970), but it is clear that big sagebrush control is short-lived and treatments must be repeatedly applied to maintain the grass (Harniss and Murray 1973; Thilenius and Brown 1974) and disturbed or treated big sagebrush habitats are vulnerable to overgrazing (Braun and others 1976).

onflicts also arise from inadequate research. ost studies attempting to analyze the effect of ig sagebrush control on sage grouse have been oo brief or too limited in scope to identify ritical sage grouse seasonal use areas before reatment. Hopefully, new study will fill in the aps.

asically, the 1977 "Guidelines for Maintenance f Sage Grouse Habitats" still apply in 1984 Braun and others 1977). However, there have been ome misunderstandings or misapplications of the Guidelines." Studies of sage grouse life history nd habitat requirements have provided information n why sagebrush treatment around strutting rounds is so detrimental to the species. The trutting ground itself is not the critical abitat in need of protection. Rather, it appears hat the winter, nesting, and rank escape cover or male feeding-loafing areas close to the trutting ground are critical. I will deal with ach of these in this report. Big sagebrush for rood-rearing habitat is of lesser importance and ill not be discussed.

INTER HABITAT

ig sagebrush makes up 95 to 100 percent of the inter diet of sage grouse from October through pril. In May, sage grouse shift from a big agebrush-dominated diet to one dominated by orbs; in September there is an opposite shift rom forbs to big sagebrush, triggered by freezing emperatures or snow accumulations (Girard 1937; riner 1939; Bean 1941; Dargan and others 1942; atterson 1952:198; Nelson 1955; Klebenow and Gray 968; Savage 1969; Martin 1970; Peterson 1970; akleaf 1971; Wallestad and others 1974). Winter locks or concentrations shift their winter range n response to snow depth and food availability. he extent of winter movement depends on the everity of the weather, topography, and egetative cover (Beck 1975). Autenrieth (1981) tributed the initial predictable movements to latability of big sagebrush, and secondly, to s availability above the snow.

ntering areas can be identified by topography, ructural characteristics, and subspecies of big gebrush. For sedentary populations, the ntering area is often located within 2 miles .2 km) of the strutting ground and nesting area. dentary populations are nonmigratory with the tal straight-line distance between brood and nter centers generally less than 10 miles (16). Sage grouse moving more than 10 miles are nsidered migratory (Baker 1978:21; Berry and Eng 35). They appear to prefer large, flat or ntle slopes of less than 15 percent (Eng and Sladweiler 1972; Jarvis 1974; Beck 1977; Autenrieth 1981). Winter-use areas are determined by amount of snow rather than affinity to a particular site.

In wintering areas, sage grouse tend to concentrate on the higher wind-swept ridges and flats where big sagebrush is available (Jarvis 1974). Southern aspects seem preferred (Beck 1977; Autenrieth 1981). There is no difference between vegetation or physical characteristics of winter roosting and feeding-loafing sites (Beck 1977; Eng and Schladweiler 1972). However, researchers have noted sage grouse selecting areas with the greatest canopy cover available. The majority of winter observations were in sagebrush with more than 20 percent canopy coverage. In Idaho, the average height was 22 inches (55.8 cm) and canopy coverage was 28.1 percent (Autenrieth 1981). This was confirmed by Schoenberg (1982) in North Park, CO, who found that the length, width, height, and canopy cover of big sagebrush plants were greater at sage grouse winter feeding-loafing sites than at any of the breeding season feeding-loafing sites.

The species and subspecies of sagebrush that seem to be preferred by grouse in the winter are black sagebrush (A. nova), low sagebrush (A. arbuscula), and certain subspecies of big sagebrush (Crawford 1960; Autenrieth 1981). Remington (1983) found in North Park, CO, that 90 percent of the plants identified as fed-upon were Wyoming big sagebrush (A. t. wyomingensis). Mountain big sagebrush (A. t. vaseyana) and alkali sagebrush (A. longiloba) made up 7 percent and 3 percent, respectively, of the remaining sagebrush plants fed upon.

Nitrogen may be an important factor in food selection. High nitrogen levels may be physiologically critical. Remington (1983) found that Wyoming big sagebrush contained more protein (14.1 percent vs. 10.8 percent) than mountain big sagebrush. There was significant variation in protein content within subspecies. Plants fed upon had higher protein than those not fed upon. Monoterpenoids content did not vary between plants of Wyoming big sagebrush fed upon and not fed upon.

Winter diet quality was high in sage grouse (protein = 15.9 percent, cell contents = 77.8 percent, ADF = 13.7 percent) relative to winter diets of other grouse, resulting in increased fat content over winter. Thus, the normal critical energy period for sage grouse appears to be the breeding-nesting period and not winter. However, there is evidence to indicate that during severe winters sage grouse lose considerable energy reserves which may influence both the duration and intensity of breeding activity.

Because sage grouse do not have a muscular grinding gizzard and select subspecies and plants low in monoterpenoids, they are adapted to avoid the harmful effects of monoterpenoids in sagebrush. Reduced digestibility and a requirement for a high-quality winter diet of big sagebrush are probably consequences.

Winter Habitat Management

Before winter habitat can be properly managed it must first be located. This should occur during moderate-to-heavy snow years. Wintering areas can be located by examining telemetry fixes, topography, or ground and aerial sightings.

After these sites have been located and verified by the presence of snow roosts the following habitat characteristics should be measured: sagebrush species and subspecies composition, plant height, percent of sagebrush cover.

If winter habitat must be disturbed, compatible sagebrush species and subspecies need to be seeded. Genotypes of big sagebrush high in protein (Welch and McArthur 1979), high in digestibility (Welch and Pederson 1981), and low in monoterpenoids (Welch and McArthur 1981) should be used.

The lack of protection of critical winter habitat has resulted in sage grouse population declines. In Montana, Pyrah (1972) found sage grouse winter use declined proportionally to the severity of big sagebrush eradication. Strip-partial kill, block-partial kill, mechanical treatments, and total-kill spray, in that order, were increasingly detrimental to sage grouse. Winter use essentially ceased in the total-kill areas. Critical winter habitats were quite vulnerable to treatment since big sagebrush control historically has been directed toward dense stands on flat to gentle slopes.

Remington (1983) suggests some management techniques for improving critical winter-use areas. These include: (1) fertilize with nitrogen to enhance the quantity and quality of big sagebrush forage (Carpenter 1976; Laycock 1982) and (2) encourage sage grouse use of Wyoming big sagebrush stands normally unavailable due to snow depth by use of snow fences or carbon black (Regelin and Wallmo 1975).

Winter Habitat Research Needs

Research that would be of greatest value in managing sage grouse winter habitat is listed below:

1. Determine the effects of various fertilizer applications, formulas, concentrations, phenology, and sagebrush subspecies on the nutritional content of big sagebrush.

2. Determine the effects of big sagebrush removal by various means on soil erosion, nutrient leaching, and soil water retention.

3. Determine the subspecies of big sagebrush as indicators of ecological sites relative to suitability for treatment by herbicide or prescribed burning.

4. Determine the characteristics of the soil or habitat type of subspecies of big sagebrush.

5. Define the soil type and moisture relationship to nutritional composition and phenology of big sagebrush.

6. Develop through genetic engineering superior big sagebrush cultivars high in protein and low in monoterpenoids.

7. Develop a data base on big sagebrush response to herbicides under varying dosages and environmental conditions, guidelines for data to be taken, and computer storage.

8. Determine the relationship between insect infestations and resistant genotypes of big sagebrush which produce natural phytotoxins or repellents and the effects of these toxins on sage grouse nutrition.

9. Determine the nutritional value of big sagebrush by age class and optimum canopy cover and morphology by age classes.

10. Determine use levels of big sagebrush by deer, antelope, or sage grouse which stimulate (if any) plant growth and vigor.

BREEDING AREAS

A second critical time when big sagebrush quantity and quality is important to sage grouse is during breeding. Strutting grounds vary greatly in topographical or physical features (Rogers 1964). Strutting grounds may be gravel pits, plowed fields, wheat stubble, salt licks, remote air strips, temporary sheep camps, paved roads, bare exposed ridges, knolls, small buttes, bare openings in big sagebrush, and dry lake beds. Sage grouse seem to take advantage of newly disturbed areas. Therefore, strutting grounds are not distinctive except that they are usually surrounded by big sagebrush cover and provide a panoramic view (Autenrieth 1981).

Adult male sage grouse first move to strutting grounds in March (Jenni 1971). Hens arrive later. Males are attracted to hens rather than their mating centers. Hens breed with individual males that are more active than other males. Hens are not attracted to geographic sites themselves. This accounts for the slight movement of grounds from year to year.

The big sagebrush surrounding the strutting grounds is critical! Big sagebrush surrounding strutting ground is used as food, loafing, and escape cover by the males. Male activity is generally restricted to these sites within .6 mile (1 km) of the strutting ground (Wallestad and Schladweiler 1974; Autenrieth 1981; Carr 1967; Rothermaier 1979; Emmons and Braun 1980). Male sage grouse select big sagebrush stands that are taller and have greater canopy coverage than random sites (Ellis and others 1984; Wallestad and Schladweiler 1974; Autenrieth 1981; Schoenberg 1982). Emmons and Braun (1980), Wallestad and Schladweiler (1974), and Autenrieth (1981) reported that 80 percent of all male locations were in big sagebrush cover of 20 to 50 percent. Big sagebrush canopy coverage averaged 30 percent on male feeding-loafing areas in Montana (Eng and Schladweiler 1972) and males were not observed in areas with less than 10 percent canopy coverage. Emmons and Braun (1980) found that cover and height at feeding-loafing areas averaged 28.1 percent and 15 inches (38.3 cm)

espectively. Schoenberg (1982) found that both cover and height were greater in use areas than n randomly chosen areas (33 percent vs. 26 ercent and cm vs. 19 cm, respectively). atterson (1952) found optimum loafing sites ere along stream bottoms, ravines, and draws.

praying big sagebrush in these male eeding-loafing areas probably resulted in some f the population declines reported by so many esearchers. Wallestad (1975) reported that a 1 percent loss of habitat adjacent to a strutting round coincided with a 63 percent decline of ales counted on strutting grounds. Strutting rounds that had averaged 54 males for 13 years ropped to 3 within 2 years after spraying, and fter that were totally abandoned. In Idaho, utenrieth (1969) observed that sprayed strutting rounds continued to be used if the surrounding esting and brood-rearing habitat was not estroyed. Others (Enyeart 1956; June and Higby 965) also noted declines resulting from land-use hanges.

he preferred solution to this problem is to dentify male feeding-loafing use areas and rotect them from big sagebrush control. This can e accomplished by radio-marking males and onitoring their movements during the breeding eason. The next best alternative is to conduct n appraisal of big sagebrush quantity and quality ithin a 2-mile (3.2 km) radius of the strutting round of sedentary (resident) populations. This ppraisal could include range site-habitat type, oil type, topography, aspect-slope, and dentifying on aerial photographs the locations of eeps, springs, and meadows. Data could be erified by site inspections. This should include dentifying subspecies of big sagebrush and the allest and greatest canopy cover on aerial hotographs.

ere protection of strutting grounds is not ssible, birds have been transplanted (Ligon 46; Wing 1951; Patterson 1952) or strutting ounds have been moved (Eng and others 1979; Tate d others 1979). Both actions require extensive bitat appraisals and telemetry studies of asonal use areas to be successful. However, the tter is more labor intensive and the outcome ss sure.

STING HABITAT

g sagebrush also is critically important during e May nesting period. Typically, hens begin sting within 10 days after breeding. The peak breeding in Utah varies, but generally occurs netime in late April. The incubation period is 2 days. The peak of hatch also varies, but curs about June 5. This corresponds with the art of livestock use on many ranges.

A ressing issue is that sage grouse hens nest most exclusively under big sagebrush (Schlater 1 2). Keller and others (1941) found that 94 p cent of located nests were under big sagebrush. S ilar results have been found by Girard (1937), P terson (1952, p. 114), Gill (1965), Gray (1967), and Wallestad and Pyrah (1974). Jarvis (1974) found 48 of 60 nests in south-central Utah were located under big sagebrush.

Hens appear to select nesting sites beneath big sagebrush that has good canopy cover and is relatively tall. Autenrieth (1981, p. 20) observed that big sagebrush plants with an umbrella effect were usually selected by the hen. He attributed this selection to improved survival of the hen and improved nest success due to protective camouflaging. "The importance of big sage cover for nesting cannot be over-estimated," he said.

Most studies indicate that the majority of nests are located under the tallest plants available in the area (Keller and others 1941; Patterson 1952:114; Trueblood 1954; Rogers 1964; Gray 1967; Klebenow 1969; Jarvis 1974; Wallestad and Pyrah 1974;). Jarvis (1974) found that hens tended to select sites with big sagebrush for nesting rather than black sagebrush sites. However, Autenrieth (1981) indicated that hens on his five areas selected something less than the greatest height and canopy cover. He believed the height and density of sagebrush in his study areas was greater than those in other study areas, and apparently height and canopy cover were not limiting factors in his areas. Thus, he postulated a threshold level of tolerance for these values.

Most researchers agree that hens nest under sagebrush plants that are taller than plants of average height in the area. Wallestad and Pyrah (1974) found the average height of big sagebrush plants where nests were located was 16 inches (40.4 cm) compared with 9 inches (23.4 cm) in surrounding stands. Similar heights over nests were reported by Patterson (1952) and Klebenow (1969). Patterson (1970) found that the average height of sagebrush at nest sites in Colorado was 21 inches (52.3 cm) while height of the surrounding big sagebrush was 13 inches (32.3 cm). Areas of big sagebrush taller than 35 inches (89 cm) were seldom used. Jarvis (1974) also found that big sagebrush used for nesting averaged 39 percent taller than adjacent shrubs. Autenrieth (1981:17) found that in all cases the nest shrubs were taller than surrounding shrubs, indicating that the hen is selecting a particular shrub. Nest shrubs ranged in height from 22.4 inches to 31.5 inches (57 cm to 80 cm) while shrubs surrounding the nest site ranged from 9.1 inches to 31 inches (23 cm to 79 cm). Basically, figures on optimum sagebrush heights for nesting provided in the "Guideline for Maintenance of Sage Grouse Habitats" (Braun and others 1977) remain valid. Optimum heights are between 6.7 inches (17 cm) and 31.1 inches (79 cm).

Sagebrush canopy cover is an important variable associated with the selection of nest sites. Canopy cover percentages of 20 to 40 are selected as nesting cover (Patterson 1952, p. 114; Klebenow 1969; Martin 1970; Jarvis 1974; Wallestad and Pyrah 1974; Autenrieth 1981).

Recent research by Peterson (1970) in North Park, CO, confirmed these figures, but Schoenberg (1982) studying the same area in 1979-80, found a slightly higher (44 percent) canopy cover for big sagebrush used for nesting. In Idaho, Klebenow (1970) found that nesting ceased on newly sprayed areas with less than 5 percent live big sagebrush canopy cover. Nesting was nearly nonexistent in older sprayed areas with about 5 percent live big sagebrush cover.

Big sagebrush canopy cover is positively correlated with hatching success. Wallestad and Pyrah (1974) found 31 successful nests had greater than average sagebrush cover within 24 inches (61 cm) of the nest and these were located in stands with a higher average canopy cover (27 percent) than unsuccessful nests (20 percent). No nests were found where canopy coverage was less than 15 percent. Jarvis (1974) attributed the significantly higher nest success under big sagebrush compared to black sagebrush on his Utah study area to the greater canopy cover at big sagebrush sites. Although Autenrieth (1981,p.20) found that for 165 nests in Idaho there was no significant difference between the height or canopy cover of the nest shrub on successful versus unsuccessful sites, he suggested this was because sagebrush height and canopy cover were not limiting. His study areas had taller big sagebrush and greater canopy cover than study areas in Montana.

The proximity of nesting to strutting grounds depends upon the proximity of quality and quantity of preferred nesting habitats to the strutting ground (Autenrieth 1981). In migratory populations, the majority of nesting may not occur within 2 miles (3.2 km) of the strutting ground. In fact, some evidence suggests that some hens move as much as 15 to 20 miles (24.1 to 32.2 km) from the strutting ground to nest.

Most viable sage grouse populations are considered sedentary or resident. That is, they move less than a 10-mile (16-km) radius in 1 year. In these populations, it appears that the majority of nesting occurs within 2 miles (3.2 km) of the strutting ground (table 1). Autenrieth (1981) found that when good nesting cover was available near the strutting ground, the nesting radius tended to be less than when cover was sparse and only in clumps. Poor nesting habitats result in longer migrations by the hen to quality nesting sites, which increased the probability of predation and reduced survival.

The proximity of riparian areas may be another important variable determining nest site selection. Some researchers have concluded or implied that readily available water is essential for optimum nesting habitat and that the availability of water influences nest site selection (Griner 1939; Patterson 1950, 1952; Trueblood 1954; Carr 1967). However, Keller and others (1941) indicated in their Colorado study that there was no definite preference for sites close to water. Klebenow (1969) and Wallestad (1975) did not mention free water as a component of optimum nesting habitat in Idaho and Montana. Batterson and Morse (1948) and Nelson (1955) also indicated that nest distribution was not affected by water. Autenrieth (1981) found no relationship between water or meadows and proximity of nests. Jarvis (1974) found almost all of his nests within 1.3 miles (2.1 km) of a lake, reservoir, or pond, but only about one-third were within one-half mile (.8 km) of a water source. Although water may not be a limiting factor on some sage grouse habitat, water developments should be protected, maintained, or constructed within 1 mile of each other on nesting habitats in zeric zones (less than 10 inches [25 cm] annual precipitation).

It appears that species of sagebrush is an important determinant of nest location. A significant positive correlation is indicated in the literature for number of nests located and big sagebrush overstory. Big sagebrush is extremely important for nesting cover (Girard 1937; Keller and others 1941; Patterson 1952; Gill 1965; Gray 1967; Wallestad and Pyrah 1974).

The effect of grazing on nesting habitats is important. Autenrieth (1981, p. 20) found that understory ground cover contributed to a microclimate warmer than air temperature 3 ft

Table 1.--Results of a literature review of the percent of sage grouse nests found within a specified radius of the strutting ground

Location and reference	Sample size	Percent of nests located a given distance from the strutting ground: 1 mi (1.6 km)	1.5 mi (2.5 km)	2 mi (3.2 km)	3 mi (4.8 km)	4 mi (6.4 km)	5 mi (8.0 km)	6 mi (9.7 km)	8 mi (12.9 km)
Northwest Colorado, Gill (1965)	23	--	--	87	--	--	--	--	--
Southwest Montana, Martin (1970)	5	--	--	80	--	--	--	--	--
Montana, Wallestad and Pyrah (1974)	--	68	--	--	--	--	--	100	--
South Idaho, Autenrieth (1981)	306	28	--	59	73	85	96	97	100
Southwest Wyoming, Berry and Eng (1985)	17	--	53	--	59	--	--	--	--
Southcentral Utah, Jarvis (1974)	62	--	--	66	76-81	--	--	--	--

(1.9 m) above the nest. Nest temperatures dropped less during hen absence where understory was greatest. Sheep grazing from December through May on nesting areas should be regulated to prevent overuse of grasses and forbs.

Topographical features may also be important in nest site selection. Schlatterer (1960) found that sage grouse hens in eastern Idaho showed some preference for islands of big sagebrush on rock outcrops, surrounded by grassy openings. No nests were found on north-facing slopes, and southern slopes seemed to be preferred. Keller and others (1941) found no definite preference for either slope or exposure in North Park, CO, but they observed that the highest nesting success occurred in little draws where the bottoms were covered with low-growing vegetation. Jarvis (1974) made similar observations on his study area in Utah. Optimum nesting habitats were located where numerous dendritically arrayed shallow draws were separated by relatively broad flats (Jarvis 1974). The upper extremities of these small, shallow tributaries having a northerly or easterly aspect seem to be preferred. Nests were frequently located just above the bottom of the drainage or in shallow basins at its head. The majority of the nests were in the more robust vegetation associated with these sites (heavier and higher than the surrounding cover).

Slope appeared to be important. Almost 69 percent of the nest sites were situated on relatively flat sites of 5 percent or less slope. An additional 1 percent were on 5 to 20 percent slopes. Hens avoided steeper slopes.

Unlike Schlatterer's (1960) or Keller and others (1941) findings, Jarvis (1974) found a fairly definite preference for northern aspects. About 5 percent of nests were located on slopes facing north or northeast as opposed to only 14 percent facing south or southeast. Jarvis thought that this was due to the more mesic conditions of northern aspects.

Management recommendations for nesting habitats should include:

1. Give 1-year written advance notice to the appropriate wildlife agency of intent to treat so ie can be appraised.

2. Identify nesting habitat by marking-telemetry studies and habitat appraisals and determine what are limiting habitat components.

3. Maintain or protect nesting habitats, especially those nearest breeding complexes.

4. Limit disturbances and sagebrush control programs on nesting areas during April-May-June breeding-nesting periods.

5. Regulate grazing on nesting habitats.

6. When reseeding drilling pads and reclaimed mine sites, include dryland legumes like alfalfa (Medicago spp.), sainfoin (Onobrychis vicaefolia), and vetches (Astragalus spp.) in seed mixes.

7. Do not block-spray, but preferably use ground application in irregular-shaped patterns, avoiding taller denser patches of sagebrush within 2 mi (3.2 km) of strutting ground with irregular margin for maximum edge and diversity. Openings created in uniform habitats of sagebrush should not exceed 50 yd (45.7 m) in diameter with optimum diameter of 5 to 10 yd (4.6 to 9.1 m). Treatment areas should not exceed 40 ac (16 ha). The goal of treatment should be to not reduce sagebrush cover below 20 percent and 3,400 plants per acre. If strip-sprayed, leave strips should be at least twice as wide as kill strips and at right angles to prevailing wind or slope of the land (Braun and others 1976).

8. Do not treat sagebrush on sites where costs exceed expected benefits.

9. Do not treat sagebrush on sites with less than 20 percent canopy cover of sagebrush.

Research that would be of greatest value in managing sage grouse on nesting habitat is listed below:

1. Determine rate of reestablishment of sagebrush after treatment via photo-trend plots and vegetative measurements.

2. Test hypotheses for reasons hens select nest sites and nest success with:
   a. proximity to strutting grounds
   b. proximity to brood habitat
   c. nest site quality-concealment
   d. nest site temperature-microclimate
   e. distance to water
   f. sagebrush characteristics, e.g. canopy volume, canopy cover, height, age by multivariate analysis
   g. ground cover-understory
   h. camouflaging
   i. morphology-age class

3. Assess impact of application rates, phenology, date of application, and herbicide (2,4-D-Tebuthiuron) on live sagebrush canopy cover 1 mo, 1 yr, and 5 yr after treatment; and assess effects on sage grouse reproduction, distribution, and density.

4. Make nest preference studies on subspecies of big sagebrush.

5. Determine minimum viable population for specific population and minimum habitat needed to sustain populations.

6. Determine the relationship between xeric sage grouse habitats and the tendency of sage grouse populations to migrate.

7. Assess the effect of various grazing systems on winter and breeding-loafing habitats.

8. Study the effect of prescribed burns on nesting habitat.

CONCLUSIONS

Big sagebrush is extremely important to sage grouse especially during winter and spring. The protection or maintenance of wintering, breeding (male feeding-loafing areas), and nesting sagebrush habitats is essential for the survival of sage grouse populations. For sedentary populations, protecting these habitats within 2 mi (3.2 km) of the strutting ground is very important. This does not mean that all sagebrush within 2 mi (3.2 km) of all strutting grounds must be protected. The 2-mi (3.2 km) limit set in the 1977 "Guidelines" was not intended to be rigidly substituted for a good habitat reconnaissance and appraisal. One-year lead time is critical if this appraisal is to be adequate and of value.

The 1977 "Guidelines" still apply in 1985 for sedentary populations, but for migratory populations, critical seasons use areas must be identified through marking-telemetry studies.

There is no substitute for an adequate habitat appraisal to identify sacrifice areas where big sagebrush can be treated without significant harm to the sage grouse population. To accurately predict the effects of big sagebrush manipulation on sage grouse populations we need a comprehensive understanding of sage grouse seasonal use areas and which are limiting. This requires lead time, which is a basic professional courtesy extended by the Federal land management agency to the State Wildlife agency. There must be a cooperative spirit and a commitment to get the job done by both types of agencies.

Sage grouse depend on big sagebrush to fulfill their basic requirements. The future of sage grouse depends upon our ability and willingness to maintain sagebrush habitat types. I tend to agree with Pyrah (1966) who wrote 20 years ago that:

> "A continued lack of concern is prevalent in most agencies which are causing the serious shrinkage of sage grouse habitat. They show little regard for sage grouse or other wildlife when its welfare is weighed against the demands of the livestock monoculture being benefitted."

Wildlife biologists in land managing agencies need to take their multiple-use charge in the Federal Land Management and Policy Act more seriously.

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SEASONAL MOVEMENTS AND HABITAT SELECTION OF SAGE GROUSE IN SOUTHERN IDAHO

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ABSTRACT: In 1980 and 1981, 31 sage grouse hens were captured at the U.S. Sheep Experiment Station, Dubois, ID, and fitted with radio transmitters to document movement and selection of habitat. Similarities between habitat by months and areas were determined by discriminate analysis. Data were gathered on the effects of predation and weather on nesting and brood production. The sage grouse were found to be migratory. One hen moved at least 106.0 air miles (160.9 air/km) between nesting, summering, and wintering areas, and then in 1981 nested within 82 ft (25 m) of her 1980 nest.

INTRODUCTION

Sage grouse (Centrocercus urophasianus) have developed a migratory or nonmigratory strategy for survival depending on topography, vegetative cover, available water, and winter climatic conditions (Beck 1975). Wallestad (1975) stated that wintering, nesting, and brood habitats for sage grouse in the Yellow Triangle area of Montana were interspersed and required no long seasonal movements by these birds. In contrast, sage grouse in southeastern Idaho travel up to 49.7 mi (80 km) between summer and winter range (Pyrah 1954). Sage grouse that nest near the Red Road (Clark County) site in southeastern Idaho have distinctly different wintering, nesting, and brood rearing areas (Dalke and others 1963), while sage grouse on the Idaho National Engineering Laboratory (INEL) site (Jefferson Co.), also in southeastern Idaho, nest on or near their winter range and then move to summer areas (Connelly and others 1981).

Several good reviews are available that discuss the seasonal importance of big sagebrush to sage grouse (Patterson 1952; Johnsgard 1973; Wallestad and Pyrah 1974; Wallestad 1975; Braun and others 1977). There is good documentation that certain stands of big sagebrush may have too much cover or be too tall or not have enough component interspersion to serve as ideal habitat for sage grouse during specific periods of their yearly cycle (Martin 1970; Peterson 1970; Call 1974).

Seasonal sagebrush cover for sage grouse include the following recommendations: winter, 20 percent (Eng and Schlandweiler 1972; Wallestad 1975); brood, 8.5 to 14 percent (Gill 1965; Klebenow 1969; Martin 1970; Autenreith 1981); nesting, 20 to 40 percent (Patterson 1952; Gray 1967; Klebenow 1969; Wallestad and Pyrah 1974).

Recommendations for management of habitat on sage grouse ranges may differ depending on whether the flock is migratory or nonmigratory. Nonmigratory flocks generally use one area for nesting, brood production, and wintering while migratory flocks use different areas for one or more activities. Proper management of habitat for sage grouse should include consideration of seasonal and functional uses in each area.

In this study, we observed the year-round movements of selected female members of a migratory sage grouse flock in southeastern Idaho. Nesting and summer habitats were measured and comparisons were made in relationship to migration.

STUDY AREA AND METHODS

The study was initiated on the U.S. Sheep Experiment Station (USSES) 5 mi (8 km) north of Dubois, Clark Co., southeastern Idaho. The USSES provides spring-fall grazing for domestic sheep and has an average elevation of 5,657 ft (1 700 m). Twenty-six sage grouse leks were located in 1980 and 1981 on the 40 mi^2 (103.6 km^2) USSES. Major shrub species include big sagebrush (Artemisia tridentata) and three-tip sagebrush (A. tripartita). Tailcup lupine (Lupinus caudatus) and arrowleaf balsamroot (Balsamorhiza sagittata) are two of the prominent forbs. Principal grasses are bluebunch wheatgrass (Agropyron spicatum) and thickspike wheatgrass (A. dasytachyum).

During summer, sage grouse used areas near Kilgore and Humphrey, Clark Co., ID. The Kilgore area, 19 mi (30 km) northeast of the USSES, is

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ypified by cultivated dryland alfalfa-grass hay surrounded by big sagebrush rangelands at an average elevation of 6,400 ft (1 951 m). Water in the dryland farm area is abundant due to a high water table and numerous streams. Humphrey is 21.1 mi (33.8 km) north of the USSES and is egetated by sparse big sagebrush with much of the rea having been sprayed at some time with 2,4-D erbicide. The elevation at Humphrey is about ,000 ft (2 134 m). Water is always available ithin short distances. Cattle and sheep graze he Humphrey and Kilgore areas during summer onths. Winters are severe with all shrubby egetation being mostly covered with snow.

outhwestern Clark County and northwestern efferson County are used by sage grouse in inter. The area is sagebrush-dominated rangeland nterspersed with irrigated, cultivated farmland. ig sagebrush and black sagebrush (A. nova) are he major shrubs with black sagebrush occupying ie rocky areas and windswept ridges.

iirty-one sage grouse hens (including three iveniles) were captured between March 25 and June , 1980, and during the same dates in 1981. Each en was fitted with a 2-oz (57-g) backpack radio ransmitter to document movement and selection of ibitat. Nine hens were recaptured in late August 980, and refitted with active transmitters. Two f the nine were again refitted in early spring 981 so they could be monitored for a complete nnual cycle. Hens were captured at night with d of a spotlight and long-handled net. strumented hens were located as often as ssible (usually weekly) from the ground during mmer. During winter, grouse were located monthly from aircraft, followed by ground cation, if possible.

summer, measurements of habitat were taken each me a radioed hen was located. The percentage ver of each plant species (with the exception of asses which were combined) was estimated in 12 8 by 19.7-inch (20- by 50-cm) plots (Daubenmire 59), three in each cardinal direction, 4.9 ft .5 m) apart, using the observation point of the rd as the center reference point for placement the plots. In addition, the percentage of bare ound, rock, litter, and the height of the llest shrub of each species in each plot were asured.

sting habitat was quantified by measuring the ight, width, and length of each woody species in a 100-ft^2 (9.3-m^2) circular plot, with the nest as center point. Also percentage cover of forbs, ss, and each shrub species was estimated in a 8-ft^2 (1-m^2) circular plot around each nest. height and species of shrub directly above the t were recorded, as well as the distance from nest to the lowest canopy above the nest. tistical analyses were made by using group parison t-tests or paired t-tests unless erwise stated (Johnson 1976).

nts of cocks and hens were taken periodically each lek (strutting or breeding area) on the ES throughout the 1980 and 1981 seasons.

Counting began one-half hour before sunrise and continued to 1 hr after sunrise (Jenni and Hartzler 1978). Leks were approached via truck. The research counted and classified all observed birds with the aid of 7 x 35 binoculars. Locations of historical leks, as well as numbers of birds per lek, were obtained for 1966 (Klebenow, unpublished data) and 1979-80 (Green, unpublished data).

RESULTS AND DISCUSSION

Movements

In 1980, the instrumented sage grouse hens nested an average of 1.7 mi (2.7 km) from the nearest lek; this was significantly ($P \leq 0.25$) farther than the 0.5 mi (0.8 km) nesting distance in 1981 (table 1). Ten of 15 hens had probably commenced nesting when they were captured in 1981 compared to only three of the 13 in 1980.

Ten of 13 hens in 1980 nested within 1.9 mi (3 km) of the lek nearest to their nest site; however, two hens traveled over 6.2 mi (10 km) before nesting (table 1). These two hens, one a yearling and the other an older adult, nested at elevations of 6,549 ft (1 996 m) and 6,460 ft (1 969 m). These elevations were 869 ft (265 m) and 800 ft (244 m) higher, respectively, than the nearest lek site.

The movements of two hens, 478 and 473, were monitored for over 1 yr (fig. 1, table 1). Hen 478 was periodically located from April 14, 1980, to August 5, 1981; during this period she traveled 106.0 air mi (169.6 km). She moved 20.2 mi (32.2 km) from her nesting area to the Humphrey area for the summer. In the fall, she traveled 47.2 mi (76.5 km) to the wintering area on the INEL site. In the spring, she returned to the USSES and nested within 82 ft (25 m) of her nest from the previous year.

Hen 473 traveled 73 air mi (117 km) from her nest site in 1980 to the 1980-81 wintering area and back to her nest site in 1981, nesting within 820 ft (250 m) of her nest from the previous year.

Following nesting, instrumented female sage grouse used three distinct summer areas (figs. 2 and 3). In 1980 and 1981, eight hens used the Kilgore area, six used the Humphrey area, and eight stayed just north of the USSES. In 1980, adult females moved an average of 16.4 mi (26.2 km) to the summer range from the breeding ground. This distance was significantly greater ($P \leq 0.01$) than the 6.3 mi (10.1 km) traveled by the yearling female sage grouse (table 1). Overall, in 1980 and 1981, the average distance traveled from the nesting area to the summer range was 12.6 mi (20.1 km) and the increase in elevation was 1,464 ft (446.2 m) (fig. 4). Hens left the USSES about June 23 and arrived at their summer ranges usually within a few weeks.

Table 1.--The distance of movement and the elevation of the radio-instrumented sage grouse hens captured at the USSES, Dubois, ID, in 1980 and 1981

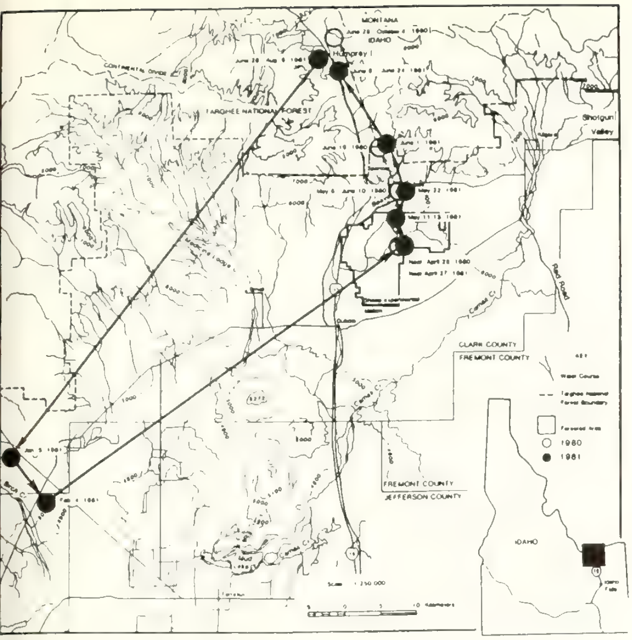
Bird number	Lek to nest distance	Nest elevation	Breeding ground to summer range	Summer elevation	Summer range to winter range	Breeding ground to winter range	Yearly distance	Winter elevation
	(miles)	(ft)	(miles)	(ft)	- - - - - - - - - (miles) - - - - - -			(ft)
1980								
465	0.2	5,580						
467	0.1	5,690	18.0	6,390	31.1			5,249
468	3.8	5,920	6.2	6,060	24.1			5,098
469	0.6	5,685	17.6	6,319	33.5			5,049
470	0.8	5,690	11.7	6,260				
471			18.7	6,490				
473	0.5	5,850	19.2	6,400	33.9	20.1	73.2	4,902
475	6.6	6,460	20.9	8,100				
478	0.1	5,690	10.0	6,915	47.3	38.7	106.0	5,000
479	0.5	5,665	12.9	6,370				
480	0.4	5,685	18.8	8,160				
Sub. mean	1.4a[1]	5,971	16.4a	6,745a	34.0	29.4	89.6	5,059
	(2.2 km)	(1 765 m)	(26.2 km)	(2 056 m)	(54.4 km)	(47.1 km)	(143.4 km)	(1 542 m)
466	0.2	5,660	5.0	5,980	31.2			4,850
472	1.4	5,950	5.2	5,980				
474	6.3	6,549						
476			8.8	6,220				
Sub. mean	2.6a	6,053a	6.3b	6,060a	20.6			4,850
	(4.1 km)	(1 845 m)	(10.1 km)	(1,847 m)				
Total mean	1.7a	5,850a	14.1a	6,590a	31.4a	31.2	84.9	5,025
	(2.7 km)	(1 783 m)	(22.5 km)	(2 008 m)	(50.2 km)	(49.9 km)	(135.9 km)	
1981								
465A	0.7	5,560	17.9	7,200				
471A	0.3	5,655	15.3	8.600	13.1			6,250
472A	0.3	5,700	16.7	5,600				
621	0.8	5,620	5.1	5,900	43.8	39.8		4,800
626	0.5	5,660	15.6					
627	1.5	5,840	14.5	6,700				
628	0.7	5,620	4.4	5,980	26.2			5,049
478	0.2	5,680	17.9	6,800				
469A	0.3	5,700	3.5	5,870				
473	0.4	5,869						
473A	0.1	5,680	7.4	6,800				
474A	0.3	5,880	9.7	7,260				
480A	0.4	5,700	2.3	5,751				
624	0.9	5,580						
629	0.2	5,670						
Mean	0.5b	5,660b	10.9b	6,620a	27.7a			5,367
	(0.81 km)	(1 736 m)	(17.4 km)	(2 018 m)	(44.2 km)			(1 636 m)

[1] a and b = the same letter for the sub. mean or total mean in a column indicates no significant difference; different letters denote significant differences ($P \leqslant 0.05$).

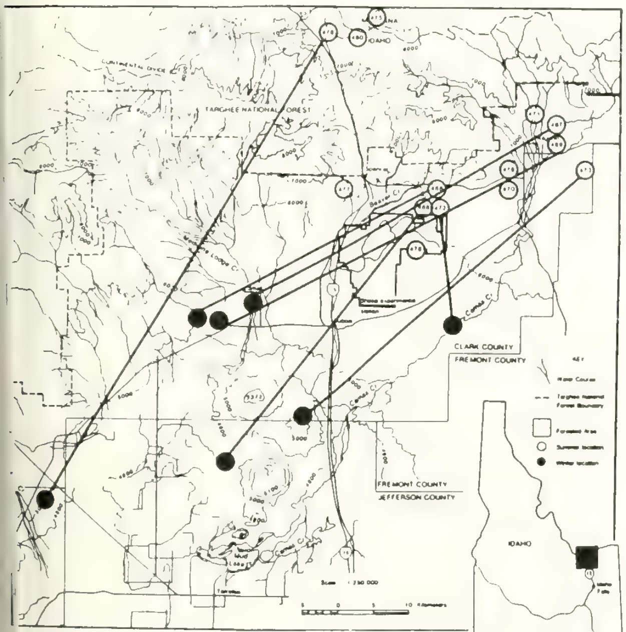
Some birds moved almost continuously through August; others established a relatively small home range. Of those that established home ranges, the largest was 1,762.0 ac (7.1 km^2); the smallest was 22.2 ac (0.09 km^2), and the average was 704.2 ac (2.85 km^2).

Movements from the summer range to the winter range, in 1980 and 1981, are illustrated in figures 3 and 4. The average distance from summer to winter range was 10.1 mi (48.2 km) with a drop in elevation of 1,463.9 ft (446.2 m) (table 1, fig. 4). The greatest distance traveled from the winter area to the breeding grounds was 39.8 mi (63.7 km). Six of nine birds monitored during the winter either died or their radios stopped transmitting. Therefore, they may not have reached their final wintering area.

In 1980, five of seven hens were still at their summer areas on October 31. The other two were their summer locations on October 4, but had be to move to their winter areas by October 31. Three of five birds were still at their summer locations on October 23, in 1981. All the instrumented sage grouse moved in a southwesterly direction to wintering areas. Of the nine birds located during winter, five used areas dominated by black sagebrush, usually on exposed ridgetops.



igure 1.--Movements of hen 478 from April 25, 980, to June 24, 1981, in Clark and Jefferson ounties, ID (from Hulet 1983).



F ure 2.--Summer and winter locations of 14 radio i trumented female sage grouse captured at the U ES, Dubois, ID, 1980 (from Hulet 1983).

N ting

A rage big sagebrush cover in the 100-ft^2 (3-m^2) circular plots around the 30 measured n ts was 17.2 percent, comprising only 65 p cent of the relative cover of the 26.2 p cent total shrub cover (table 2). Of the

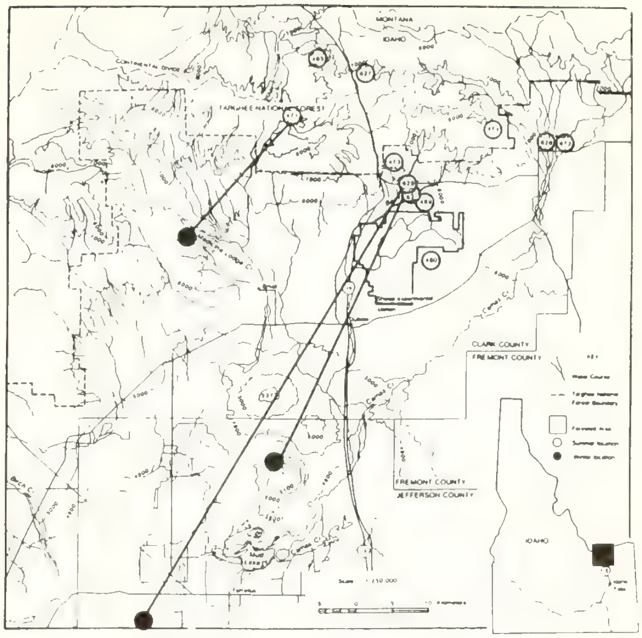


Figure 3.--Summer and winter locations of 11 radio instrumented sage grouse captured at the USSES, Dubois, ID in 1981 (from Hulet 1983).

total 87 percent canopy cover measured in the 10.8-ft^2 (1-m^2) plots around each nest, only 49 percent was big sagebrush, and this represented just 56 percent of the relative cover.

For 30 nests around which habitat measurements were taken, the main shrubs above the nests were big sagebrush (52 percent), three-tip sagebrush (14 percent), antelope bitterbrush (*Purshia tridentata*) (17 percent), and dead sagebrush (10 percent). Seven percent of the nests had no shrub cover; these were located beneath the canopy of Russian thistle (*Salsola iberica*). These data differ from what Patterson (1952) found in Wyoming where 92 percent of 300 nests were found beneath the canopy of big sagebrush. Gill (1965) and Wallestad and Pyrah (1974) found, respectively, that 92 percent and 100 percent of nests were under the canopy of big sagebrush. Hen 478 nested under big sagebrush in 1980 and under antelope bitterbrush in 1981, while hen 473 nested under three-tip sagebrush in 1980 and big sagebrush in 1981. These two grouse seemed to have little or no preference for the shrub species whose canopy they nested beneath. The 17.2 percent big sagebrush cover for nests on the USSES was less than the 23.4 to 38.1 percent found by Autenrieth (1981) in southern Idaho. This is probably due to the greater availability of different shrub species suitable for nesting cover on the USSES.

Sage grouse chose to nest beneath the canopy of shrubs that were taller than average for the immediate area. For example, the average shrub height, 18.4 inches (46.7 cm), for all shrubs combined above nests was significantly greater ($P \leq 0.05$) than the 9.8 inch (25.0 cm) average

Table 2.--The percent cover of the shrubby vegetation 10.8 ft^2 (1 m^2) and 100 ft^2 (9.3 m^2) around the nests of radio-instrumented sage grouse captured at the USSES, Dubois, ID, in 1981 and 1981. Included are the height of certain shrubs and percent cover of grass and forbs 10.8 ft^2 (1 m^2) around the nest

	Percent cover					
	100 ft^2 (9.3 m^2)			10.8 ft^2 (1 m^2)		
Vegetation	1980	1981	Mean	1980	1981	Mean
Amelanchier alnifolia	0.4		0.2			
Artemisia tridentata	14.1	19.2	17.2	35.9	57.0	49.0
Artemisia tridentata (dead)				6.5	9.5	8.5
Artemisia tripartita	3.0	1.1	1.9	22.9	5.3	12.0
Chrysothamnus nauseosus		0.3	T[1]		0.3	0.2
Chrysothamnus viscidiflorus	0.9	0.7	0.8	1.4	0.6	0.9
Purshia tridentata	6.3	2.5	4.0	28.5	9.3	16.6
Rosa woodsii	0.2	T	0.1			
Symphoricarpos oreophilus	0.2		0.1			
Tetradymia canescens	1.8	1.8	1.8		0.4	0.2
Gutierrezia sarothrae	0.1	T	T			
Total shrub cover	27.1	25.7	26.2	95.2	82.0	87.2
Grass cover				12.0	18.5	16.0
Forb cover				15.3	23.7	10.9
Artemisia tridentata						
Height (inches)	9.5	9.2	9.4			
Mean shrub height (inches)	9.8	9.9	9.8			

[1]T = trace.

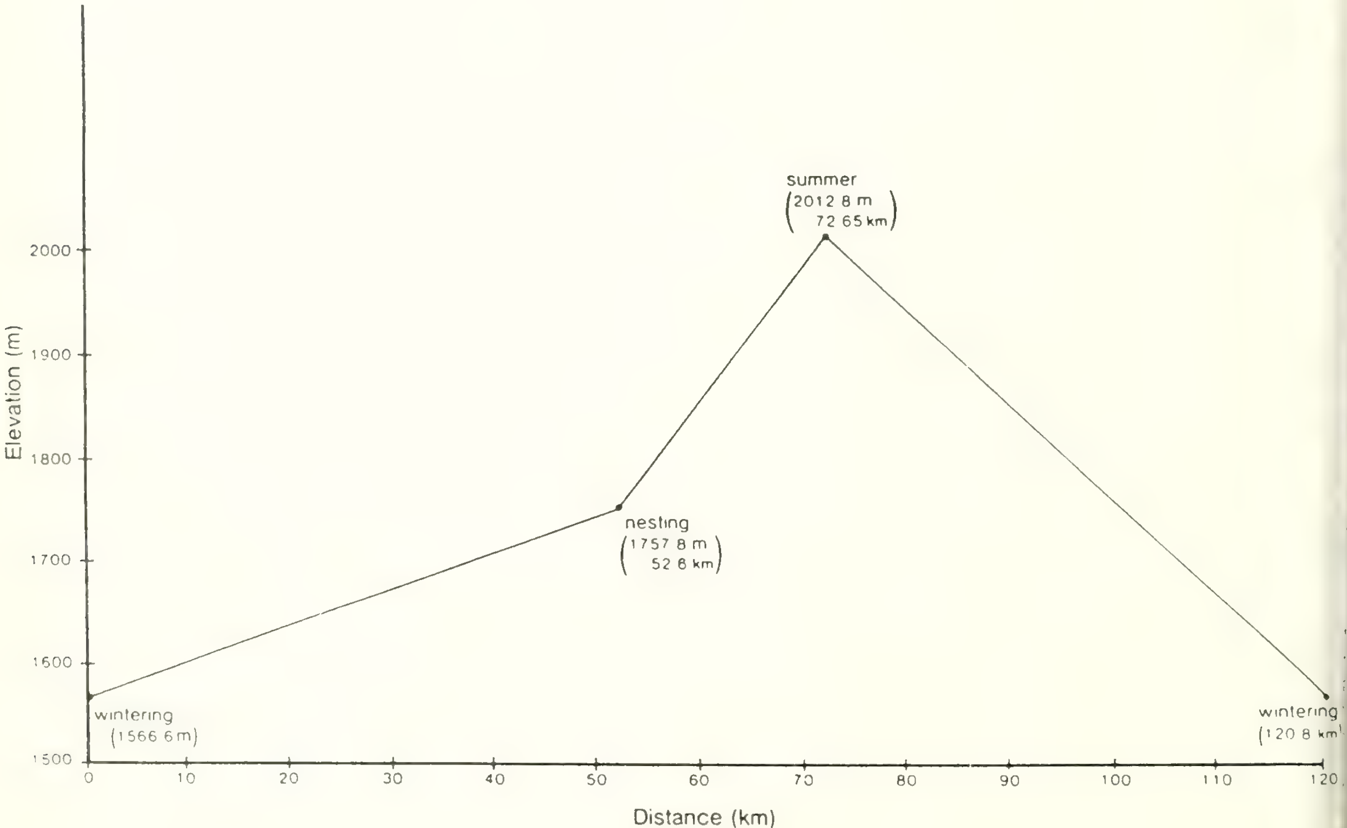


Figure 4.--Comparison of elevation and distance traveled to wintering, nesting, and summering areas of 28 radio-instrumented sage grouse hens captured at the USSES, Dubois, ID, in 1980 and 1981 (from Hulet 1983).

ight for shrubs in the 100-ft^2 (9.3-cm^2) ircular plots around the nest. Similarly, verage height for big sagebrush over nests was 7.6 inches (44.8 cm) compared to the 9.4 inch 23.9 cm) average height of big sagebrush within ne 100-ft^2 (9.3-m^2) plot around each nest. verage height of the shrub above the nest, ercent cover of grass, forbs, and all shrubs 10.8 ft^2 (1 m^2) around each nest for 1980 and 981 are detailed in table 2. The percent cover or all shrubs located within the 100-ft^2 (9.3-m^2) lot around the nests in 1980 and 1981 also is isted in table 2.

redation

leven nests were destroyed by predators in 1980 nd 1981, with the Uinta ground squirrel Spermophilus armatus) being responsible for most nests or 64 percent) of the destruction. Three the four hens that renested had their nests estroyed by predators. In 1981, four successful est sites were compared vegetatively to five nest tes that had been destroyed by predation (table . Within a 100-ft^2 (9.3-m^2) circular plot round each nest, predator-destroyed nests had a

ble 3.--Comparison of shrub characteristics 100 ft^2 (9.3 m^2) and 10.8 ft^2 (1 m^2) around five predated nests and four successful nests in 1981 at the USSES, Dubois, ID

aracteristics	Predated nests n=5	Successful nests n=5
10 ft^2 (9.3 m^2) around nest		
an shrub cover (percent)	30.0a[1]	25.8a
an shrub height (inches)	9.4a	9.3a
an big sagebrush cover	20.6a	17.2a
.8 ft^2 (1 m^2) around nest		
an shrub cover (percent)	92.6a	72.0a ($P \leq 0.10$)
an shrub height (inches)	20.9a	11.0b ($P \leq 0.025$)

[1] and b in the same row denotes significant fference ($P \leq 0.05$).

eater (although not significant) total shrub er, big sagebrush cover, and total height of shrubs than nests not destroyed by predators. hin a 10.8-ft^2 (1-m^2) area around the nest, the ub height was significantly ($P \leq 0.025$) taller the total shrub cover was greater ($P \leq 0.20$) those nests destroyed by predators. These a indicate successful nests were located in as of lower shrub cover and height than those ts destroyed by predators. This contrasts to dings of Wallestad and Pyrah (1974) in Montana re successful nests had significantly ($P \leq$ .05) greater sagebrush cover within 23.6 inches cm) of the nest and within a 200-ft^2 (9.3-m^2) plot around the nest than those of unsuccessful nests.

Leks

Only two of 12 leks located in 1966 on the USSES were still active in 1981; 14 new leks had been established (fig. 5). This casts doubt on the long-term survival of leks on the USSES.

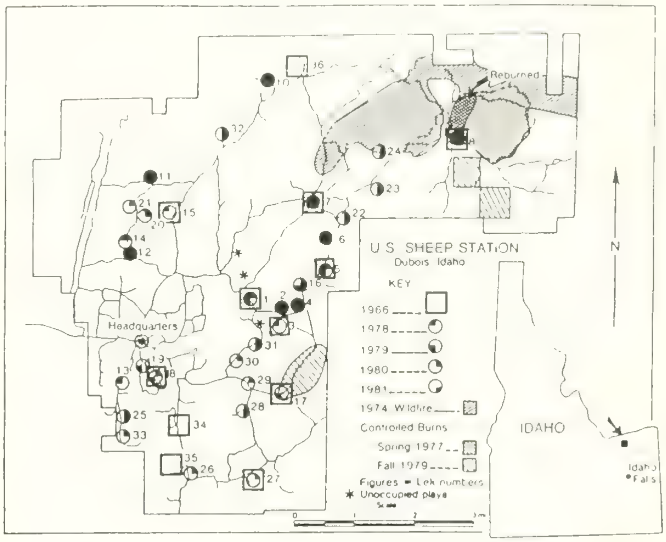


Figure 5.--Locations and dates of active leks in the U.S. Sheep Experiment Station, Dubois, ID, from 1966 to 1981. Location of recent wildfire and prescribed burns and the location of three unoccupied playas are also shown (from Hulet 1983).

Four of the active leks established since 1966 had some relationship with fire (either prescribed or wildfire). A 1,919 ac (777 ha) wildfire in July, 1974, burned approximately 29 percent of the area within a 1.9 mi (3 km) radius of lek site 24. This new lek was established as early as 1971, 1,312 ft (400 m) inside the burn area. In April, 1980, it had the largest concentration of male birds (51), compared to all other leks on the USSES. Lek site 8, burned by a 1,919 ac (777 ha) and a 647 ac (262 ha) wildfire and prescribed burn, respectively, has been active since 1966.

Forty-one percent of the area within a 1.9 mi (3 km) radius around these two leks had been burned. Another lek site was burned in a small prescribed burn in the fall of 1979, but it was still active in the 1980 mating season (15 males, 9 females on March 23). This lek was not used in 1981, probably because the crested wheatgrass (A. cristatum) planted in 1980 was not grazed to allow for after-fire rejuvenation and the 1980 growth of over 15 inches (38 cm) covered the entire lek site in 1981. The final

lek site was abandoned after a prescribed burn in 1979. Since 1966, prescribed burns or wildfires apparently helped create one lek, caused desertion of two, and had no noticeable effect on the other.

Migrations

During the summer months, the instrumented sage grouse hens moved to higher and more moist areas. A five-step discriminate analysis showed we can discriminate between the three summer areas (Kilgore, Humphrey, and northern USSES) with 82.3 percent accuracy (table 4). The discriminate analysis used 79 habitat variables (including plant species) obtained from Daubenmire plots at locations of radio-instrumented grouse during June, July, and August 1981.

Table 4.--Discriminating between the USSES, Humphrey, and Kilgore in southeastern Idaho in 1981. Percent of "grouped" cases correctly classified was 82.3 percent

Actual group	No. of cases	Predicted group membership USSES	Humphrey	Kilgore
USSES	47	45 95.7%	2 4.3%	0 0.0%
Humphrey	20	6 30.0%	14 70.0%	0 0.0%
Kilgore	13	6 46.2%	0 0.0%	7 53.8%

No convergence was obtained when a discriminate analysis was used to compare individual locations of female sage grouse in June, July, and August. However, by combining July and August samples, we could correctly classify samples taken in June versus July and August 96.2 percent of the time. This indicates that vegetation differs greatly from spring to mid- and late-summer. Observed movements of hen sage grouse to new areas in July, after annual forbs mature and dry out, reflect this difference.

Records of the Idaho Fish and Game Department show there are 137 known sage grouse leks in Clark, Lemhi, and Jefferson counties that are within migratory range of sage grouse that nest on the USSES (Autenrieth 1981). Sage grouse that nested on the USSES could thus have nested at one of three other major lek and nesting areas. These three areas are: the INEL site, Medicine Lodge, and the Red Road. Most of the birds that wintered on the north end of the INEL site also nested there and then moved up the Birch Creek drainage during summer (Connelly and others 1981). Birds that nested on the Medicine Lodge drainage generally moved to Snowline, MT, or Humphrey, ID, for the summer (Gray 1967). The sage grouse studied by Dalke and others (1963) nested near the Red Road and moved into the Kilgore and Shotgun Valley area. In comparison, sage grouse on the USSES used wintering areas occupied by all of the above-mentioned groups and part of the summer areas used by grouse from Medicine Lodge and Red Road.

Bird 478 wintered on the INEL site and bypassed perhaps 68 leks and two major breeding sage grouse populations to nest at the USSES. One wonders why she would move 39 mi (62 km) to nest at the USSES when she could have found suitable nesting and breeding areas on the INEL.

DISCUSSION

Further research should be directed toward monitoring movements of hens whose nesting areas have been destroyed to determine how the hens respond when they return the following year. In addition, chicks born to hens with established migratory routes should be monitored to see if the chicks return to the same nesting and summer areas as their mother. Results may help explain how chicks acquire essential migratory traditions and whether there are migratory and nonmigratory birds within the same breeding population.

One of the largest leks on the USSES was established 5 yr after a 1,919 ac (777 ha) wildfire burn in 1974. Although this large lek was created several years after the fire, much nesting habitat near the lek was destroyed for a much longer period of time. Further study should be directed to determining the positive and negative effects of various-sized prescribed burns on breeding and nesting behavior of migratory sage grouse.

After leaving the nesting areas, hen sage grouse seemed less restrictive in selecting summering habitats. For example, big sagebrush cover ranged from 5.0 percent to 17.4 percent in the three areas used by the USSES sage grouse. Discriminate analysis showed that we could distinguish between the three areas 82.3 percent of the time. In summer, sage grouse were found in barley and hay fields as well as in big sagebrush with a canopy cover of 44.4 percent. Hen 474 was found on August 21, 1981, under a Douglas-fir (Pseudotsuga menziesii). Our data indicate the habitat sage grouse utilize during the summer is more variable than that required during the nesting period.

Because the population of sage grouse nesting at the USSES is migratory and uses different habitats during nesting, brooding, and wintering seasons, the USSES should be managed for minimal disruption of essential nesting, breeding, and early brooding activities. Habitat management for wintering sage grouse at the USSES would be of lesser consideration since this is not a major wintering area.

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USE OF ARTEMISIA AND CHRYSOTHAMNUS BY PRONGHORNS

Jim Yoakum

ABSTRACT: Pronghorns use Artemisia and Chrysothamnus for food and cover. The amount of forage these plants provide varies greatly. It is highest in the pronghorn's northern range and much lower in southern rangelands. On some pronghorn ranges, these shrubs provide more feed than any other herbage. They are especially valuable as forage during winter months when snow covers low vegetation. These shrubs also provide critical protective cover for newborn pronghorns. This important pronghorn-shrub relationship requires further study. Management recommendations are provided for maintenance and restoration of these shrubs on pronghorn range in the Great Basin.

INTRODUCTION

Today sagebrush (Artemisia spp.) and rabbitbrush (Chrysothamnus spp.) occur throughout most of the American pronghorn antelope's (Antilocapra americana) occupied habitat (figs. 1, 2, and 3). These shrubs have provided forage and cover for antelope for centuries (Yoakum 1978).

A review of the literature reveals that these shrubs are important sources of food for pronghorns, especially on shrub-grassland steppes (tables 1 and 2). Less use is made on grasslands and deserts.

This paper reviews the importance of sagebrush and rabbitbrush to the pronghorn as forage and protective cover for fawns, and recommends practices for maintaining and enhancing these two shrubs on pronghorn range.

PRONGHORN REQUIREMENTS FOR VEGETATION

The pronghorn's vegetation requirements have been identified for the sagebrush-grasslands of the Great Basin (Yoakum 1978) and the shortgrass prairies (Yoakum 1984). Based on dietary studies and pronghorn densities on preferred rangelands, it became apparent that pronghorn distribution

Table 1.--Estimated percent consumption of sagebrush and other Artemisia spp. in pronghorn dietary studies

Vegetative community and references	Season of use				Total
	Winter	Spr.	Sum.	Fall	Annua[illegible]
Sagebrush-grasslands					
Hansen 1982	12	38	37	33	29
Koerth and others 1984	16	3	14	20	13
Mason 1952	87	65	32	71	64
Severson 1966	78	ND[1]	30	49	52
Yoakum 1958	83	58	35	54	56
Shortgrass prairies					
Dirschl 1963	10	20	17	85	33
Mitchell and Smoliak 1971	15	7	20	20	15
Schwartz and Nagy 1976	ND	57	23	20	50

[1]ND = no data.

Table 2.--Estimated percent consumption of rabb[illegible]brush in pronghorn dietary studies

Vegetative community and references	Season of use				Tot[illegible]
	Winter	Spr.	Sum.	Fall	Ann[illegible]
Sagebrush-grasslands					
Hansen 1982	1	2	1	1	
Koerth and others 1984	-	-	-	-	
Mason 1952	1	2	-	-	
Severson 1966	12	ND[1]	30	28	[illegible]
Yoakum 1958	-	3	6	-	
Shortgrass prairies					
Did not occur in any studies					

[1]ND = no data.

and abundance were correlated with the variety and abundance of forbs and shrubs. Such data allow managers to recommend key plant species for grazing plans and seed selections for restoration projects.

Pronghorn habitat requirements are specific to each vegetative community. Optimum pronghorn habitats in the Great Basin shrub-grasslands

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ve from 5 to 20 percent of ground cover of rubs with a mean height of 18 inches (38 cm). shortgrass prairies, shrub-ground cover is 1 5 percent. Shrubs must be available in the ght combination with all other biotic factors order to provide optimum habitat for onghorns. Too little or too much of any one ecies may limit pronghorn production or rvival. This is especially true for sagebrush. certain areas of the Great Basin, pronghorns not occupy areas where sagebrush makes up 60 90 percent of the vegetative cover.

RAGE

onghorns are opportunistic herbivores selecting e most palatable and succulent forage available any given time. Annual diets vary depending the availability of plants in a specific area. rbs and shrubs are used predominantly yearlong. asses are used very little (Salwasser 1980).

gebrush

thout a doubt, sagebrush and other Artemisia ecies are one of the most important plant oups consumed by pronghorns. This statement n be made for the grasslands of Alberta and lorado as well as for the shrubland steppes of egon and Nevada. Table 1 documents this well, ve of eight annual food habit studies list temisia as more than 30 percent of total diet. other plant genus was used as much. Wherever temisia was available, it was consumed during . four seasons of the year. The availability shrubs for forage during severe winters has en directly linked to pronghorn survival yless 1969; Barrett 1982).

much or too little of any habitat component be detrimental to wildlife (Dasmann 1964). s is especially true for shrubs on pronghorn itat. A shortage of shrubs can increase elope mortality during winters when snow ers most vegetation and only shrubs protrude provide forage, and also when there are too plants for adequate cover for fawns. Too y shrubs, on the other hand, impede rapid ape from predators and compete for moisture and l nutrients needed to produce other preferred age species. A plant community containing e to 10 shrub species making up 5 to 20 cent of the ground, provides optimum browse on nghorn shrubland steppes.

ferred rangelands in southeastern Oregon monly have low sagebrush (Artemisia arbuscula) summer rangelands and black sagebrush temisia nova) on winter rangelands. Areas inated by big sagebrush (Artemisia tridentata) less used, probably because of tall growth of plant. The components of sagebrush munities essential for optimum pronghorn itat are illustrated in figure 1.

istrom and others (1973) listed the following etation criteria for optimum pronghorn itats on shrub-grassland steppes.

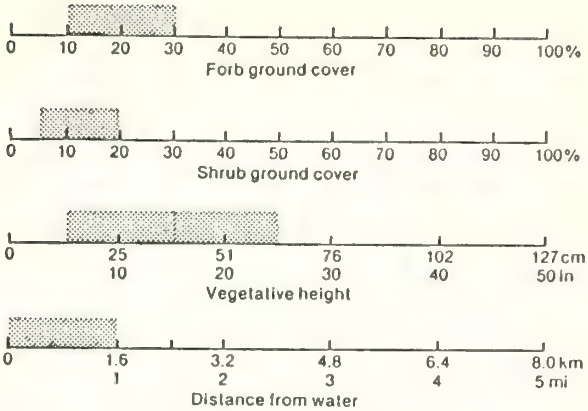

Figure 1.--Components of pronghorn habitat in the sagebrush steppe. Habitat becomes optimum when all components occur together within the bounds marked by bars. (Kindschy and others 1982.)

1. Community to be relatively open (cover less than 40 to 60 percent).

2. Height of shrubs (or other vegetation) not to average more than 18 inches (38 cm).

3. Composition usually consisting of:

   a. 10 to 20 percent sagebrush
   b. 5 to 15 percent other shrubs (including rabbitbrush)
   c. 25 to 35 percent forbs
   d. 40 to 60 percent grasses

4. Preferred species of shrubs for browse are:

   a. Artemisia tridentata (big sagebrush)
   b. A. filifolia (sand sagebrush)
   c. A. frigida (fringed sagebrush)
   d. A. cana (silver sagebrush)
   e. Chrysothamnus viscidiflorus (Douglas rabbitbrush)

In summary, Sundstrom and others (1973) stated that preferred pronghorn habitat in sagebrush-grasslands is characterized by (1) the presence of Wyoming big sagebrush and/or silver sagebrush in combination with other preferred sagebrushes and Douglas rabbitbrush, and (2) the general environmental factors associated with these plant communities. They also stated that antelope density and reproduction appeared to be correlated directly with available amounts of preferred species of sagebrush and associated forbs.

The pronghorn's most northern endemic rangelands are the shortgrass prairies of Alberta and Saskatchewan in Canada. A 6-year study of habitats in Alberta by Barrett (1982) disclosed that wintering antelope herds were largest on rangeland containing silver sagebrush. These key wintering areas, where sagebrush frequently formed more than 75 percent of the diet, were critical to antelope survival.

Deming (1963) provided a provocative perspective of the relationship of sagebrush to pronghorns by stating that the importance of sagebrush in the antelope diet may be due to availability rather than palatability. He further stated that some of the best ranges, with the highest antelope densities, in the past and today, are rolling grasslands, and that sagebrush ranges generally do not produce these highest densities of pronghorns. This has since been substantiated by Yoakum (1978) who documented that two-thirds of the total antelope population occupy grasslands and one-third use shrub-grasslands.

Rabbitbrush

Rabbitbrush is usually considered an undesirable forage plant for livestock; however, it is a highly preferred species for pronghorns (fig. 2).

It should be managed as a needed component on pronghorn rangelands. Table 2 indicates that rabbitbrush comprised more than 1 percent of pronghorn year-long diets on shrub-grasslands. For certain areas, such as the Red Desert in Wyoming, rabbitbrush was consumed slightly more than sagebrush (Severson 1966). Douglas rabbitbrush was preferred over sagebrush during summers and early fall. One reason for less use of rabbitbrush than sagebrush during the winters was that more of the rabbitbrush was covered with snow. According to Severson (1966): "The most important species in the antelope diets were Douglas rabbitbrush and big sagebrush." Rabbitbrush was consumed as soon as it started to grow in the spring and was used extensively until it matured in the fall. It was extremely important, comprising 30 percent of the annual diet (Severson 1966).

Figure 2.--A yearling male pronghorn feeding in a rabbitbrush-grassland community (photo by author).

Fawn Bed Sites Needs

Vegetation characteristics of pronghorn fawn bed sites were documented in Idaho (Autenrieth 1976) and Montana (Pyrah 1974). Both studies identified tall sagebrush habitats as important bed sites for fawns. However, Beale and Smith (1970) in Utah, Barrett (1978) in Alberta, Bodie (1979) in Idaho, and McNay and O'Gara (1982) in Nevada did not reach this conclusion. Beale and Smith (1970) and Bodie (1979) found high predation on fawns in tall shrublands.

Habitat requirements of pronghorn fawns require further study. Tall shrubs may provide important protective cover in some communities, but not in others. For example, shrubs often comprise less than 5 percent of vegetative cover in grasslands, yet grasslands support the highest pronghorn densities in North America (Yoakum 1978). Figure 3 illustrates low sagebrush as cover for pronghorn.

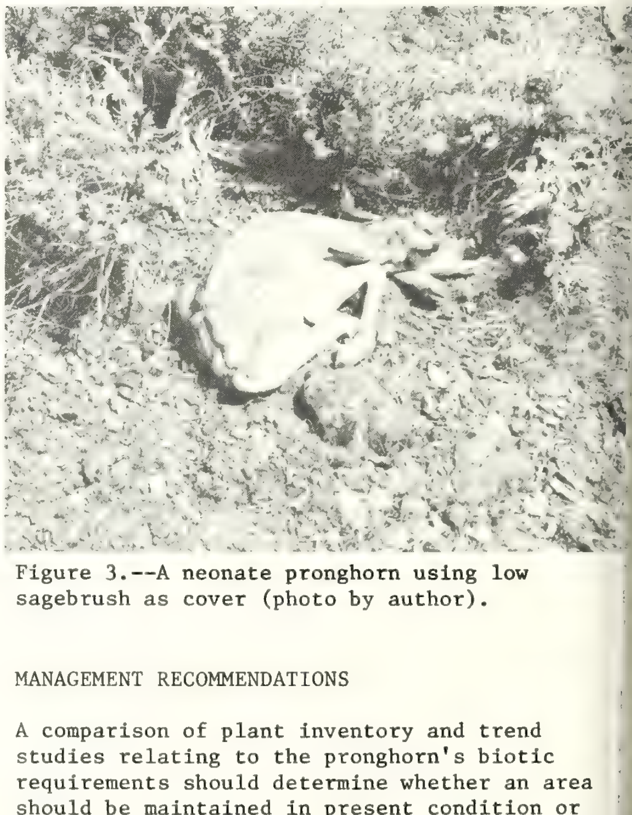

Figure 3.--A neonate pronghorn using low sagebrush as cover (photo by author).

MANAGEMENT RECOMMENDATIONS

A comparison of plant inventory and trend studies relating to the pronghorn's biotic requirements should determine whether an area should be maintained in present condition or enhanced to better meet the pronghorn's requirements for vegetation.

Maintain Habitats in Quality Condition

A cardinal rule of wildlife habitat management is when an environment is in good ecological condition, maintain it in good condition. Following this ecological rule, alone, may not meet all management objectives, such as producing maximum numbers of pronghorns. For example, some sagebrush communities in the Grea Basin are 70 percent or more shrub ground cove If this is the site's natural potential, it wi not support a large pronghorn population,

ecause with this much sagebrush, the site has a w carrying capacity for pronghorn. Management ould not expect the site to produce more onghorns. However, when inventories disclose at a site has the ecological site condition eting the habitat requirements of pronghorns, en the objective of management should be to otect and maintain the quality of that site. cannot be emphasized too strongly that where od quality natural habitat exists, management ould maintain that habitat quality.

hance Habitats in Low Quality Condition

a rangeland is in good condition, it is oducing its natural potential of pronghorns; erefore, manipulation of vegetation cannot be stified as a means to improve conditions for onghorns. Only on those sites which provide adequate vegetative conditions, but which ovide the right combination of other habitat ctors, can manipulation be justified. onghorns thrive on rangelands in a subclimax getative condition (Kindschy and others 1982). ch conditions can be the result of wildfires used by lightning, grazing by herbivores, or getation manipulation. Optimum pronghorn bitats contain a variety of grasses, forbs, and rubs. Range improvement projects that provide milar mixed forage classes can best meet onghorn requirements.

tensive areas of dominant (more than 30 percent ant composition), tall (exceeding 24 inches [60]) sagebrush and rabbitbrush communities ovide low-density rangelands for pronghorns, mpared to similar sites with fewer shrubs and e grasses and forbs. These shrublands can be ated to make the vegetal structure more vorable for pronghorns.

ub control has been a major practice on stern rangeland during the past four decades. moving sagebrush with large brushland plows was method used extensively. Chaining, another hanical shrub control method, does not kill as y shrubs as plowing and is less damaging to ive grasses and forbs; therefore, chaining is e favorable for pronghorn rangeland agement.

ause sagebrush and rabbitbrush are important pronghorns, these plants should not be minated. Illegal spraying of sagebrush on lic lands in Wyoming resulted in an inistrative law decision requiring the ellant to replant sagebrush for wildlife amond Ring Ranch, IBLA 73-48, August 17, 3).

preferred plant species are scarce, pronghorn itats can be seeded artificially. Scarcity of ored plants can result from repeated wildfires troying endemic sagebrush-grassland types opold 1966), and also when mining operations ip off the natural vegetation. Under such cumstances on public lands, the Surface ing Act of 1977 requires rehabilitation of the e to its original vegetative conditions, including the replanting of sagebrush and rabbitbrush.

Complex mixture seedings (Plummer and others 1968) serve pronghorns best because they reestablish a mixed plant community of grasses, forbs, and shrubs, approximating natural conditions. They meet the vegetation requirements of pronghorns and many other wildlife species more than monotypic seedings.

We have the technology to successfully plant sagebrush and rabbitbrush on western rangelands. Thousands of acres have been successfully planting during the past three decades.

DISCUSSION AND CONCLUSIONS

Today we have a wealth of information about the relationship of pronghorn habitat requirements. Knowledge is sufficient for managers to maintain and enhance rangelands for pronghorns. For the shrub-grassland steppes, this means the retention of endemic sagebrush and rabbitbrush. In many areas, the survival and abundance of antelope are directly related to these two shrub species. Their importance as native species cannot be emphasized too strongly. Pronghorns and many other species of wildlife have been dependent on these shrubs in natural ecosystems for eons.

Manipulation of the environment to meet human needs is the major factor affecting wildlife habitat quality today. It is imperative for the future of wildlife that these needs be compromised on sagebrush-rabbitbrush rangelands.

Sagebrush and rabbitbrush are important forage and cover shrubs directly related to the survival and abundance of pronghorns on shrub-grassland steppes. When these endemic shrubs are eliminated from the natural ecosystem by repetitive fires, mining activities, or planned conversion practices on public lands, it is mandated by Public Laws that these species be reestablished.

Sagebrush and rabbitbrush have existed on western rangelands for centuries; they are a part of the natural vegetative community. Pronghorns and many other native wild animals rely on these shrubs for survival. Today's land ethic dictates that land managers perpetuate these native plants and animals as a part of ecosystems in good natural ecological condition.

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BLACK SAGEBRUSH RESPONSE TO GRAZING IN THE EAST-CENTRAL GREAT BASIN

Warren P. Clary

ABSTRACT: Results from a variety of sites with different sheep or sheep-cattle grazing histories show a rather consistent reduction in black sagebrush cover compared to areas that were not grazed. Low-elevation black sagebrush experienced the greatest cover reduction. Moderate use during midwinter or alternate year use during midwinter appear to be compatible with maintaining black sagebrush cover.

INTRODUCTION

Winter grazing of the low-shrub cold desert ranges by livestock began in the late 19th century soon after settlement of the intermountain West. Grazing at seasons other than winter was possible only in a few places near reliable water. Winter use was possible because the light snowfall provided water for the animals, and snow was rarely deep enough to inhibit animal movement and foraging (Holmgren 1973). The cold desert ranges therefore :omplemented other ranges in the region which,)ecause of deep winter snows, could be grazed)nly in the summer.

[n the 1880's major herds of sheep arrived in :he area and a predominant use of the desert as ;heep winter range began. Sheep numbers were ıighest between 1905 and 1931, then began to lecline. During this period the most valuable :orage species declined in number and vigor, and .nferior species increased, greatly reducing the ;razing value of the desert (Stewart and others 940).

[ost of these lands were publicly owned and .nmanaged until the passage of the Taylor razing Act in 1934. Prior to passage of the ct, concerns about grazing impacts on winter razing land had led to the initiation of a eries of study plots in western Utah and across entral and northern Nevada. This consisted of airs of fenced and unfenced 4-acre (1.6-ha) lots. They were established in 1932 through 939, roughly at the point that grazing came nder some control. The Desert Experimental Range was also established in western Utah during this period (1933) to provide a place for the study of winter livestock grazing (Holmgren 1973).

Black sagebrush (Artemisia nova) is the sagebrush most closely associated with low-shrub cold desert (salt desert shrub) habitats in the Great Basin. It is a small, spreading, aromatic shrub 6 to 18 inches (15 to 45 cm) tall. Black sagebrush is most abundant at elevations from 5,000 to 8,000 ft (1 500 to 2 400 m) on dry, shallow, stony soils often underlain by bedrock or hardpan (Blaisdell and Holmgren 1984). Black sagebrush populations in the east-central Great Basin are highly preferred by sheep (Hutchings and Stewart 1953), pronghorn (Beale and Smith 1970), and, for certain cultivars, by deer (Welch and others 1981).

This study was conducted to determine the response of black sagebrush to sheep and cattle grazing in the east-central Great Basin.

STUDY SITES AND METHODS

Four-Acre Plots

In 1981 and 1982, data were collected from nine pairs of 4-acre (1.6-ha) plots located in Millard County, UT, and White Pine County, NV. The selected plot pairs were limited to those which contained black sagebrush. The paired plots were located approximately 100 yards (91 m) apart. Each plot contained 40 permanent 200-ft^2 (18.6-m^2) subplots. Plant cover by species was determined using the point-observation-plot method (Stewart and Hutchings 1936). Four of the nine plot pairs occurred within the boundaries of the Desert Experimental Range (DER). The grazed member of these pairs received moderate grazing use averaging 2.1 acres (0.8 ha) per sheep month. Grazing use on public land sampled by the remaining five plot pairs is unknown, however, use records for allotments surrounding the DER suggest moderate levels of stocking may have been approached for the last two decades. Earlier use on at least some of these areas was described as heavy (Hutchings and Stewart 1953). Plot pairs were considered to be blocks in a randomized block analysis of variance. Analyses were performed to determine if plant cover of grazed and ungrazed plots differed after 42-50 years, during a period of some control of grazing.

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One pair of 2-acre (0.8-ha) plots, containing 20 200-ft^2 (18.6-m^2) subplots each, was also sampled and used in the climatic comparison described later.

Black Sagebrush Corner

In 1981 and 1983 across-the-fence comparisons were made in different locations. These were located along the west side of the Desert Experimental Range (DER) in an area known as Black Sagebrush Corner. The DER side of the fence had received moderate late fall and early winter grazing which averaged 2.1 acres (0.8 ha) per sheep month since 1933. No specific record of grazing use is available for the Bureau of Land Management (BLM) area outside the DER boundary fence, but Hutchings and Stewart (1953) reported that use was heavy and recollections of older sheepherders were that use continued into the spring when forage plants are more easily damaged (Blaisdell and Holmgren 1984). Forty 200-ft^2 (18.6-m^2) plots on each side of the fence were sampled. Plant cover differences were assessed using unpaired t-tests.

Bud Sagebrush Corner

Another area on the west side of the DER known as Bud Sagebrush Corner contained black sagebrush, but only in the bottoms of small ephemeral washes. Another across-the-fence comparison was made on six of these washes. They were sampled using five 200-ft^2 (18.6-m^2) plots on each side of the DER boundary fence. The area on the DER side was grazed every other year in midwinter at a rate of 1.5 acres (0.6 ha) per sheep month. However, the amount of use received by the washes themselves is unknown. Unpublished data from the first 24 years of the grazing comparison suggest that utilization of black sagebrush in the entire Bud Sagebrush Corner grazing unit was not greater than in other grazing units on the DER (Holmgren and Hutchings, unpublished data). The area outside of the fence was grazed annually by the same sheepmen that grazed outside the Black Sagebrush Corner, until 1979, when cattle grazing began outside the Bud Sagebrush Corner. Differences in plant cover within the washes were analyzed by paired t-test using samples within the same wash as members of a pair.

Climatic Scale

A climatic scale for the study sites was computed as the product of elevation (ft) times precipitation (in) divided by 1,000 to reduce the size of the numbers. Relative change in black sagebrush cover on grazed plots in relation to control plots was regressed against this climatic scale. All available data were utilized--the nine 4-acre (1.6-ha) plot pairs, one pair of 2-acre (0.8-ha) plots, and the black sagebrush and bud sagebrush corner locations for which the DER portion of the comparisons was considered the control. Locations used in this study varied from 5,640 ft (1 720 m) to 6,400 ft (1 950 m) in elevation, and from 6.0 in (15 cm) to 8.5 in (22 cm) in annual precipitation received.

RESULTS

Four-Acre Plots

Significant differences had developed in plant cover on grazed and ungrazed plots during the 42-50 years since establishment (table 1). Tota[l] plant cover was less on grazed than ungrazed plots (P<0.10). This reduction of cover occurre[d] almost entirely within the shrub group. Cover o[f] black sagebrush was strongly depressed (P<0.01). Other shrubs as a group showed a moderate increase (P<0.05), presumably in response to reduced black sagebrush competition (fig. 1). The most abundant shrubs in this group were shadscale (Atriplex confertifolia), low rabbitbrush (Chrysothamnus viscidiflorus ssp. puberulus), winterfat (Ceratoides lanata), and broom snakeweed (Gutierrezia sarothrae). Forbs showed no significant differences between grazed and ungrazed sites. Grasses were somewh[at] more abundant on grazed plots (P<0.10), probabl[y] in response to a reduction in black sagebrush.

Table 1.--Plant cover of grazed and ungrazed black sagebrush sites

Plants	Percent cover Grazed	Percent cover Ungrazed	Probability
Shrubs	2.56	3.47	<0.05
Black sagebrush	1.36	2.79	<.01
Others	1.20	.68	<.05
Forbs	.09	.19	NS
Grasses	.59	.36	<.10
Total	3.24	4.02	<.10

Black Sagebrush Corner

The comparison here is of moderate (usually December) use on the DER versus heavier use th[at] continued into the critical spring period on Bl[M] land. The two data sets from Black Sagebrush Corner show similarities and differences (tabl[es] 2 and 3). Significantly greater amounts of bl[ack] sagebrush (P<0.01, 0.10) and bud sagebrush (Artemisia spinescens) (P<0.10, 0.05) occurred [on] the DER side of the fence. At location 1, tot[al] cover (P<0.01) and shrub cover (P<0.01) were greater on the DER side, but low rabbitbrush (P<0.01) and grasses (P<0.05) were greater on [th]e BLM side. At location 2, total cover, shrub cover, and low rabbitbrush cover were not different, although winterfat (P<0.10) and grasses (P<0.01) were greater on the BLM side. One forb, King budbeak (Cordylanthus kingii), [wa]s very abundant on the DER side in 1983 (P<0.05)

A

B

Figure 1.--Black sagebrush dominates the ungrazed plot (A) while grasses and other shrubs dominate the grazed plot (B).

Table 2.--Plant cover at location 1, Black Sagebrush Corner, in 1981

Plants	Percent cover DER	BLM	Probability
Shrubs	6.19	3.24	<0.01
Black sagebrush	5.54	1.92	<.01
Bud sagebrush	.13	.04	<.10
Low rabbitbrush	.15	.98	<.01
Others	.37	.30	NS
Forbs	.08	.48	NS
Grasses	.34	.47	<.05
Total	6.61	4.19	<.01

Table 3.--Plant cover at location 2, Black Sagebrush Corner, in 1983

Plants	Percent cover DER	BLM	Probability
Shrubs	6.67	6.04	NS
Black sagebrush	3.38	2.04	<0.10
Bud sagebrush	.34	.09	<.05
Low rabbitbrush	2.02	2.38	NS
Winterfat	.89	1.40	<.10
Others	.04	.13	NS
Forbs	.66	.23	<.05
King budbeak	.26	.07	<.05
Others	.40	.16	NS
Grasses	1.30	2.30	<.01
Total	8.63	8.57	NS

Bud Sagebrush Corner

This comparison is of grazing every other year in midwinter at a fairly heavy stocking rate (DER) to winter-long grazing each year (BLM). Black sagebrush responded strongly to this difference in grazing regimen by developing and maintaining substantial cover ($P<0.05$) on the DER side, and being almost entirely replaced by rabbitbrushes (low rabbitbrush and shortleaf rubber rabbitbrush [Chrysothamnus nauseosus ssp. leiospermus]) ($P<0.05$) and broom snakeweed ($P<0.05$) on the BLM side (table 4). The near 1:1 replacement of black sagebrush resulted in no differences in total shrub cover or total plant cover between grazing treatments. This area differed from the ones discussed above in that no increase in grasses appeared where a reduction in black sagebrush occurred.

Table 4.--Plant cover in dry washes, Bud Sagebrush Corner

Plants	Percent cover DER	BLM	Probability
Shrubs	3.02	2.88	NS
Black sagebrush	1.50	.06	<0.05
Broom snakeweed	.25	.85	<.05
Rabbitbrush	.67	1.56	<.05
Others	.60	.41	NS
Forbs	.01	.00	<.10
Grasses	.66	.56	NS
Total	3.69	3.44	NS

Relationship to Local Climate

The study areas showed significant differences in average cover of black sagebrush. Closer examination of the individual study locations reveals that the degree of grazing response

varied substantially. The proportional difference in black sagebrush cover was greatest in locations which were at the lower, drier edge of the black sagebrush elevational distribution (fig. 2). At higher elevations within the black sagebrush distribution where annual precipitation was greater, black sagebrush cover changed little under grazed conditions.

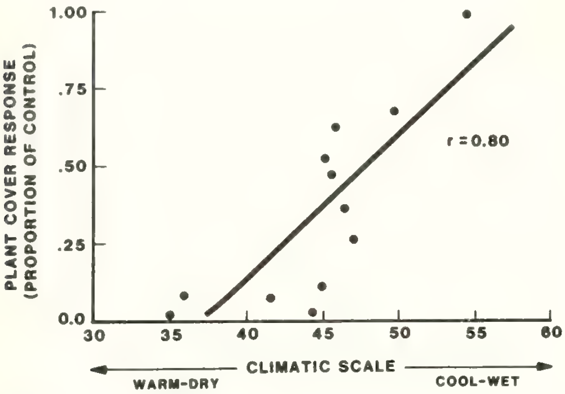

Figure 2.--Black sagebrush response to grazing in relation to climatic variation.

The differences in response may simply be due to the fact that black sagebrush is less tolerant of grazing use in drier, more stressful sites. However, assuming the lower elevation black sagebrush does experience more utilization, a question of interpretation is whether greater use occurs there because black sagebrush is part of a mixed plant composition (Cook and others 1951) or because plants in the more arid sites taste differently. Welch and others (1981) evaluated deer preferences for four accessions of black sagebrush and found utilization in a uniform garden varied from 0 to 60 percent. Behan and Welch (1985) found similar results (0 to 83 percent). This strongly demonstrates that genetically based differences among black sagebrush populations result in taste variation and, hence, preference differences.

Have the preference differences arisen by chance, or as a response to environment? For instance, the relationship shown in figure 2 could be interpreted to suggest drier sites cause an evolutionary selection for populations which are more preferred. In an initial test of this hypothesis, the deer utilization data of Welch and others (1981) were graphed against the approximate climatic conditions of the collection sites. The results of this limited examination were inconclusive. However, no soils data were available, and these should also be investigated as part of the environmental complex under which local plant communities evolve (Powell 1970). Basic differences in monoterpenoids (Welch and McArthur 1981) and other plant constituents potentially affecting preference may occur as an indirect plant population response to environmental pressures associated with different sites. An investigation of the ability of certain sites (climate-soil combinations) to produce more preferred genetic races should prove quite beneficial in the study of variation in natural plant populations.

CONCLUSIONS

These results from widely varying sites with differing grazing histories show that winter livestock grazing (principally sheep), even at stocking rates reduced from early-1900 levels, has had a measurable and often severe effect on black sagebrush. Earlier studies have illustrated that black sagebrush is often grazed more heavily by sheep than most other forage shrubs on winter ranges (Green and others 1951; Cook and Stoddart 1953). In addition, black sagebrush is one of the plants most severely impacted by defoliation (Cook and Child 1971).

Winter grazing by sheep in the lower portions of the black sagebrush elevational distribution must be carefully managed if black sagebrush populations are to be maintained. Limited comparisons among different grazing regimens suggest that moderate grazing use during midwinter or alternate year use are compatible with maintenance of black sagebrush populations.

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EFFECTS OF BIG SAGEBRUSH ON IN VITRO DIGESTION OF GRASS CELL WALL

N. Thompson Hobbs, Bruce L. Welch, and Thomas E. Remington

ABSTRACT: Using nylon bags in digestion tubes, we tested the hypothesis that substances in big sagebrush (Artemisia tridentata) inhibit digestion of grass cell walls. In our first experiment, Colton accessions (A. t. ssp. vaseyana) had no effect on cell wall digestion, but plants from Benmore (A. t. ssp. vaseyana), Wingate, and Loa (A. t. ssp. tridentata) significantly depressed cell wall digestibility. In our second experiment, we found that Loa sagebrush, which had been heated to volatilize its monoterpenoid constituents, as well as untreated Hobble Creek sagebrush (A. t. ssp. vaseyana), had no effect on cell wall digestion. We conclude that some, but not all, accessions exhibit potent antimicrobial action in vitro and surmise that volatile constituents, probably specific monoterpenoids, are responsible for that action when it occurs.

INTRODUCTION

Big sagebrush (Artemisia tridentata) is frequently a dominant constituent of the winter diet of mule deer (Odocoileus hemionus) in the Rocky Mountains and Great Basin (Leach 1956; Kufeld and others 1973; Tueller 1979; Pederson and Welch 1982). Most workers agree that big sagebrush is an important forage for deer, but there is substantial disagreement about its nutritional value. Monoterpenoids in big sagebrush have been shown to inhibit or reduce microbial activity (Oh and others 1967; Nagy and Tengerdy 1968) and to retard in vitro fermentation of cellulose (Nagy and others 1964). However, Welch and Pederson (1981) found monoterpenoids were not correlated with in vitro digestion of big sagebrush. Smith (1950), Bissell and others (1955), and Dietz and others (1962) observed that winter sagebrush was readily digested in vivo.

These conflicting lines of evidence can be reconciled by the following reasoning. Big sagebrush tissue contains a highly lignified, indigestible cell wall surrounding a large and relatively digestible fraction of cell solubles (Kufeld and others 1981). Consequently, digestion of big sagebrush requires little microbial action. It follows that dry matter digestion of sagebrush is largely insensitive to antimicrobial effects of monoterpenoids. In contrast, digestion of mature grass relatively high in cell wall should be dramatically influenced by the presence of antimicrobial substances. Grass cell wall differs chemically from the cell wall of big sagebrush. Grass cell wall contains relatively higher percentages of cellulose and hemicellulose, carbohydrates that can be digested by rumen microbes. The cell wall of big sagebrush contains higher percentages of indigestible lignin that strongly limit cell wall digestion (Kufeld and others 1981; Van Soest 1981); digestion of big sagebrush appears to depend on its solubility, whereas, digestion of mature grass results from microbial action on cell wall.

Mule deer mix grass and big sagebrush in their diets, particularly during the winter and spring (Leach 1956; Kufeld and others 1973; Hobbs and others 1983). The purpose of this study was to test the hypothesis that big sagebrush contains substances that inhibit microbial digestion of grass cell wall.

MATERIALS AND METHODS

We examined effects of big sagebrush vegetative tissue on digestion of mature grass containing high levels of cell wall. Two experiments were conducted for this study. One was a five-by-five factorial design with five replications per cell. The second was a three-by-three factorial design with five replications per cell. Factors included substrate composition and substrate amount.

Experiment One

The grass we used for this experiment was a mature Timothy hay with fiber and protein levels characteristic of senescent grass (table 1). Big sagebrush vegetative tissue was supplied

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able 1.--Composition of grass used in in vitro digestions

onstituent	Percentage of dry matter
eutral detergent fiber	71.3
cid detergent fiber	43.4
ignin	4.1
rude protein	5.2
ry matter digestibility[1]	45.0
ell wall digestibility[1]	40.0

In vivo in mule deer, D. L. Baker, unpublished data.

rom four accessions of big sagebrush grown in a niform garden (Colton and Benmore A. t. ssp. aseyana, Wingate and Loa A. t. ssp. tridentata). he experiment was conducted as follows: two ylon bags were placed inside each digestion ube filled with inoculum and buffer. We esignated one bag as the treatment bag, the ther as the response bag. In the treatment bag, e placed varying amounts of big sagebrush egetative tissue (0, 0.2, 0.4, 0.6, 0.8 g of dry atter). Mature grass tissue was placed in the esponse bag in varying amounts (0.2, 0.4, 0.6, .8, 1.0 g dry matter). Treatment and response ags were paired in the digestion tubes so the otal dry matter of the pair would equal 1 g. ive combinations of digestion tubes were repared for each accession of big sagebrush. ig sagebrush vegetative tissues were collected nd processed using the procedure described by elch and McArthur (1981). This procedure reserved the volatile constituents of the big agebrush tissues. Mature Timothy hay tissues ere prepared by ovendrying at 50°C. Grass was round in a Wiley mill to pass through a ½-mm creen. Rumen inoculum was obtained from a istulated Holstein cow fed native grass hay imilar in composition to the mature grass used n this study. We estimated cell wall isappearance from the response bags ravimetrically using the in vitro digestion rocedure of Van Soest and others (1966).

xperiment Two

his experiment was conducted like experiment ne, except we used two different types of big agebrush samples in a three-by-three factorial esign. We took a sample of the Loa big agebrush and ovendried it for 24 hours at 100°C. his was done to drive all of the volatile onstituents out of the Loa tissue. The other ig sagebrush was a fresh sample of vegetative issue from another accession we call Hobble reek (A. t. ssp. vaseyana). Welch and others 1981) have reported that the Hobble Creek ccession was preferred by wintering mule deer ver 10 other accessions (Welch and McArthur 985, unpublished data). The reason for ncluding the Hobble Creek accession was to test he hypothesis that highly preferred accessions of big sagebrush do not contain substances that inhibit microbial digestion.

Statistical Analysis

We examined effects of the big sagebrush treatments by using regression analysis with dummy variables (Kleinbaum and Kupper 1978). Cell wall digestion was the dependent variable; treatment amount, the independent. Separate models were fitted for each treatment substrate. All models shared a common origin at treatment amount = 0.0. Differences among model slopes were established with "t" tests.

RESULTS

Results of experiment one showed that constituents in the Wingate, Benmore, and Loa accessions of sagebrush inhibited digestion of grass cell wall (fig. 1). We observed no difference in magnitude of treatment effects among these accessions ($P = 0.14$). Effects of the Colton accession did not differ from the grass control ($P = 0.98$). Increasing amounts of Wingate, Benmore, and Loa sagebrush caused steep, linear declines in cell wall digestion. Although increasing amounts of Colton and grass in treatment bags appeared to enhance cell wall digestion of grass in response bags, this apparent enhancement probably resulted from differences in compaction of grass in the response bag at different treatment levels. Consequently, it represents an experimental artifact rather than a real biological influence.

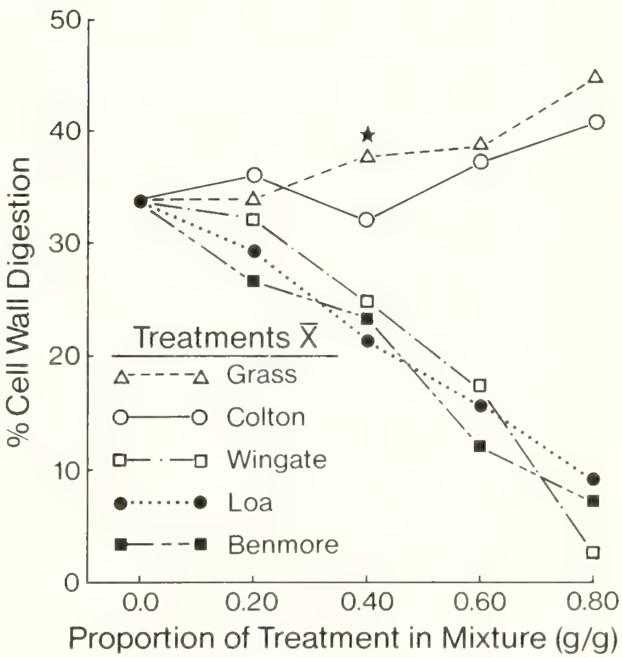

Figure 1.--Effects of sagebrush and a grass control on the in vitro digestion of grass cell wall. Star shows cell wall digestion of loose, unbagged samples. In vivo cell wall digestion of this grass in mule deer = 40.

Results of experiment two showed that removal of the volatile constituents from the sample of Loa big sagebrush removed the substances responsible for the inhibition of grass cell wall digestion detected in experiment one (fig. 2). Fresh Hobble Creek big sagebrush tissue had no effect on the digestion of grass cell wall (fig. 2).

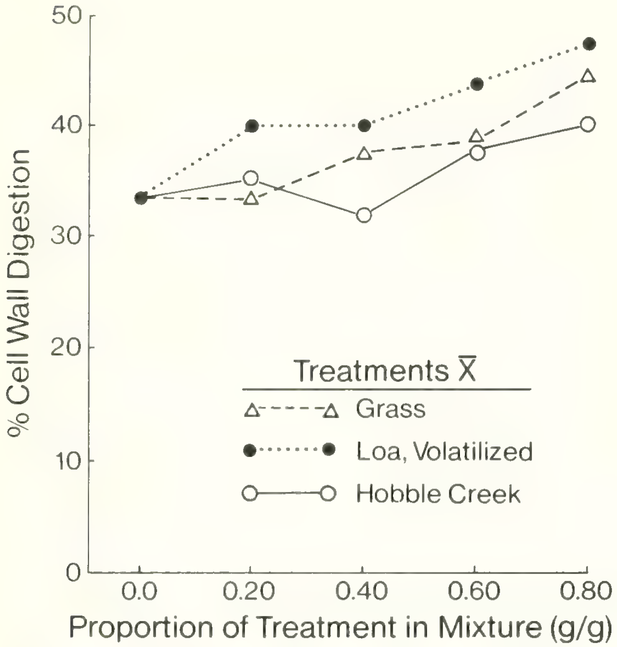

Figure 2.--Effects of Hobble Creek sagebrush, volatilized Loa, and a grass control on the in vitro digestion of grass cell wall.

DISCUSSION

Many workers have observed that herbivores show marked differences in preference among seemingly similar big sagebrush plants (Welch and others 1981; White and others 1982a; Welch and others 1983). Such differences, taken collectively, led Hanks and others (1973) to propose that two types of big sagebrush may exist side by side on western rangelands. One type is frequently eaten, the other frequently avoided.

We demonstrate a nutritional basis for this divergence in herbivore preference for big sagebrush. It appears that substances in some accessions of big sagebrush severely inhibit fiber digestion in ruminant animals. Other accessions have no inhibitory substances. These differences are associated with differences in preference. Mule deer preference for big sagebrush that shows no inhibitory effects (Colton and Hobble Creek accessions) was qualitatively greater than their preference for digestion-inhibiting accessions (Wingate, Benmore, and Loa; Welch and others 1985, unpublished data).

Several factors may mitigate the influence of inhibitory substances. These include the loss of volatile compounds from the rumen and short retention time of big sagebrush in the rumen (Cluff and others 1982; White and others 1982b; Hobbs and others 1983; Baker unpublished data 1984).

We conclude that some, but not all, accessions of big sagebrush contain volatile substances that inhibit cell wall digestion of grasses. These constituents appear to influence mule deer diet selection. Future work will focus on identifying those specific inhibitory constituents.

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Section 5. Entomology and Pathology

BIOLOGY AND DEMOGRAPHY OF THE SAGEBRUSH DEFOLIATOR AND ITS IMPACTS ON BIG SAGEBRUSH

T. H. Hsiao

BSTRACT: The seasonal history and population ynamics of the sagebrush defoliator (Aroga ebsteri Clarke) were monitored for 5 years 1971-76) at Curlew Valley, ID. Defoliator nfestation at the study site was initially high ausing severe defoliation, but declined in ubsequent years. High temperature and low recipitation were the major causes of drastic ecreases in defoliator populations. Host pecificity tests revealed that only certain pecies belonging to Artemisia subgenus ridentatae were acceptable as hosts for eeding and oviposition. Severe defoliation ould kill or reduce the vigor of big sagebrush. efoliated plants produced less foliage, had ore dead branches, and had a smaller percentage f live branches that produced flower stalks. efoliator-resistant sagebrushes offer the best anagement strategy for reducing defoliator nfestation.

NTRODUCTION

ne sagebrush defoliator (Aroga websteri larke [Lepidoptera: Gelechiidae]) is an portant pest of sagebrush. It causes varying egrees of defoliation and mortality over despread areas in Utah, Idaho, Oregon, alifornia, and Nevada (Knowlton 1960; Henry 961; Hall 1965; Artz 1972; Bechtel 1972). uring the 1960's, several studies on the efoliator and its natural enemies were onducted by Hall (1965) in northern California, ites (1964) in Oregon, and Fillmore (1965) and nry (1961) in Idaho. This report reviews some the research findings of the Desert Biome search Program, Invertebrate Process Studies, tween 1971 and 1976 concerning various aspects biology, population dynamics, and natural rtality factors of the defoliator and its fects on big sagebrush (Artemisia identata Nutt.). In view of the lack of search on this important sagebrush insect ring the past decade, it is hoped that this port will stimulate interest in the subject.

per presented at the Symposium: Biology of temisia and Chrysothamnus, Provo, UT, July 13, 1984.

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STUDY SITE

Several aspects of the field study were carried out 6 miles north of the Utah-Idaho border at Curlew Valley, a large, arid drainage basin of a former bay of the glacial Lake Bonneville, located at approximately 42 °N. latitude and 113 °W. longitude, and at an elevation of 4900 feet (1 500 m). Annual precipitation varies from 10 inches (25 cm) in the south to 13 inches (33 cm) in the north. Most rainfall occurs in spring and fall; drought conditions predominate in summer months. The valley is generally blanketed with snow in winter. Mean temperature ranges from 71 °F (21 °C) in July to 25 °F (-4 °C) in January. Maximum daily temperatures above 100 °F (38 °C) are frequently recorded from June to August. A minimum temperature of -45 °F (-43 °C) has been recorded in January. The defoliator study was conducted on a 2.5-acre (1-ha) study site near the south border of a 0.77-mi^2 (2-km^2) validation site used by the Desert Biome Program. Twenty-three plant families are found at the study site. Besides Artemisia tridentata, dominant shrubs are two rabbitbrushes, Chrysothamnus viscidiflorus and C. nauseosus. Seasonal undergrowth consists of many species of ephemeral flowers and grasses. The predominant grasses are both introductions, Bromus tectorum and Agropyron cristatum.

SEASONAL HISTORY AND BIOLOGY

Population dynamics of the defoliator were determined by weekly sampling during the spring and summer months. The sampling procedure used between 1971 and 1973 involved 40 randomly selected sagebrush branches that were measured, cut at ground level, weighed, and placed in plastic bags. In the laboratory, the defoliators were hand-sorted and their numbers and stages recorded (Hsiao 1972; Hsiao and Kirkland 1973). Beginning in 1974, the sampling and sorting techniques were improved (Hsiao and Green 1974; Hsiao and Temte 1975). Sixty plant samples were taken on each sampling date. In the laboratory these samples were initially examined for defoliator larvae by hand sorting. The number and instars of the defoliator were recorded. Samples were then placed in Berlese funnels for 3 to 5 days. The insects were collected in 70 percent alcohol, sorted, counted by instar, and added to the totals for each sample. This method increased the numbers of

early instar larvae collected. Population density was expressed as the number of defoliators per kilogram of fresh sagebrush. A Malaise trap was erected in early July near the study plot. The number and sex ratio of moths collected were recorded each week.

Figure 1 summarizes the seasonal variation in defoliator population during 1973-75 (Hsiao and Temte 1976). The defoliator has one generation a year and overwinters in the egg stage as a fully developed embryo (Kirkland 1972). Eggs are normally laid under the bark of sagebrush plants and start to hatch in late March or early April; hatching continues to mid-May. Larvae feed on sagebrush foliage for about 55 days while passing through five instars. The larvae first attack the young leaves near the terminal tips of the plants. As they grow, larvae construct web tubes that extend from the main webbing site to the terminal end of several branches. They feed on the surrounding leaves at night and remain within the protective webbing during the day. Pupation occurs in late June and adult emergence starts in early July. First instar larvae collected from the field and reared at constant temperatures of 86, 80, and 70 °F (30.0, 26.5, and 21.0 °C) became adults after 27-34, 30-35, and 40-50 days, respectively (Hsiao and Kirkland 1973).

Adult activity lasted for 2-2.5 months. Adults were found in the Malaise trap at the begining of July. Numbers peaked in the last week of July and continued at the peak level for about 3 weeks, an indication that the adults live at least this long. Five times as many males as females were trapped during early emergence (Hsiao and Kirkland 1973). The ratio gradually changed to a sex ratio of 1:1. Adults placed on caged plants became active 2 to 3 hours following dusk; maximum activity occurred between 11 p.m. and 5 a.m. They remained hidden through the diurnal period. Data from sticky traps set at various heights revealed that most moths were captured at a height between 12 and 31.5 inches (30 and 80 cm) above the ground, an indication that they tended to move near the periphery of the sagebrush crown (Hsiao and Kirkland 1973). Females captured in the Malaise trap were gravid. Examination of oocytes in the ovarioles indicated that fecundity was at least 120 eggs per female (Kirkland 1972). Egg laying in the field was noticed in late July and continued into August. Berlese funnel samplings of late-season plants indicated that relatively few larvae hatched between late August and mid-October (Hsiao and Temte 1975). The majority of eggs entered an embryonic diapause.

Figure 1.--Comparison of defoliator population densities at Curlew Valley site during 1973, 1974, and 1975.

NATURAL ENEMIES

During the study period, 10 species of parasitoids, one predator, and a Nosema disease were recorded on the sagebrush defoliator (table 1). Four species (Orgilus ferus, Phaeogenes sp., Spilochalcis leptis, and Apanteles cacoeciae) comprised 75 percent or more of the total number of parasitoids in the field population. Fillmore (1965) recovered 18 species of Hymenoptera and one species of Diptera that were parasitoids of the defoliator in southern Idaho. Of Fillmore's parasitoids, seven species are listed in table 1. The other 13 species he found were considered to be rare. Three species (Microdontomerus sp., Meteorus sp., and Microtypus sp.) (listed in table 1) ar previously unrecorded parasitoids of the defoliator.

Larvae of the clerid beetle (Phyllobaenus sp.) occasionally fed on the larvae and pupae of the defoliator. The adult stage was never found to attack the defoliator. The microsporidian disease, found in larval and pupal stages in th field and in the laboratory, accounted for less than 5 percent of the mortality in the field (Hsiao and Kirkland 1973).

POPULATION TRENDS AND MAJOR MORTALITY FACTORS

Population trends for the entire study period are illustrated by the mean population density (fig. 2) and the accumulated adults caught in the Malaise trap (fig. 3). The defoliator population initially increased from 1971 to 19.., but gradually declined between 1973 and 1975. Preliminary life tables constructed from 1971 and 1972 field and laboratory data indicated that the fifth larval instar was the "crucial trial" period for the defoliator (Hsiao and Kirkland 1973). High mortality was due to natural enemies and food shortage. Parasitism was considerable in 1971 (51.5 percent), but

Table 1.-- Natural enemies of Aroga websteri at Curlew Valley

Species	Stage attacked	Abundance
Parasitoids		
Braconidae		
Apanteles cacoeciae	Larva	Common
Orgilus ferus	Larva	Common
Meteorus sp.	Larva	Rare
Microtypus sp.	Larva	Rare
Chalcididae		
Spilochalcis leptis	Pupa	Common
Encyrtidae		
Copidosoma bakeri	Larva	Occasional
Ichneumonidae		
Temelucha sp.	Larva	Common
Diadegma sp.	Larva	Occasional
Phaeogenes sp.	Pupa	Common
Torymidae		
Microdontomerus sp.	Pupa	Rare
Predators		
Phyllobaenus sp. (Cleridae)	Larva, pupa	Occasional
Diseases		
Nosema sp. (Microsporidia)	Larva, pupa	Common

leclined to less than 10 percent after 1972 fig. 2). Thus, natural enemies have a relatively minor detrimental impact on the lefoliator. A severe infestation of the lefoliator was observed in 1972 (Hsiao and Kirkland 1973). Many sagebrushes at the study site and adjacent area were completely lefoliated by late June, causing food shortages for the defoliator. Consequently, fewer moths were caught in 1972 than in 1973 (fig. 3), even though more defoliators appeared in field amples in 1972 (fig. 2). The decline of efoliator populations in 1974 and 1975 fig. 1) is attributable to weather (Temte 1977). opulation crashes were noted on June 22, 1974 nd on July 7, 1975. The mean maximum emperatures for 2-week periods preceding the rashes were 90 °F (32.2 °C) in 1974, and 83.5 F (28.6 °C) in 1975. High daily temperature nd lack of precipitation dehydrated sagebrush oliage and made it unsuitable for defoliators t a critical period of growth. The low food alue of foliage was evident in the small size nd high mortality of field-collected pupae Hsiao and Temte 1975). The population crashes aused corresponding reductions in the number of oths caught during 1974 and 1975 (fig. 3). hese data indicate the defoliator population at he Curlew Valley site was influenced mainly by biotic factors.

OST SPECIFICITY

he defoliator is a rather restricted feeder. esides Artemisia tridentata, Henry (1961) eported natural infestations on A. tripartita, . nova, A. arbuscula, A. cana, nd A. longiloba in southern Idaho. Gates (1964) observed positive feeding on A. tridentata, A. arbuscula, A. nova, and A. cana in Oregon. Hall (1965) reared the defoliator on A. tridentata, A. arbuscula, and A. cana in California, and erroneously included rabbitbrush (Chrysothamnus nauseosus) and bitterbrush (Purshia tridentata) as hosts. While most investigators agree that big sagebrush and the species listed above are probably the principal hosts, suitability of other Artemisia species as hosts is unknown. Twenty-three Artemisia species and many varieties of these species are found in the

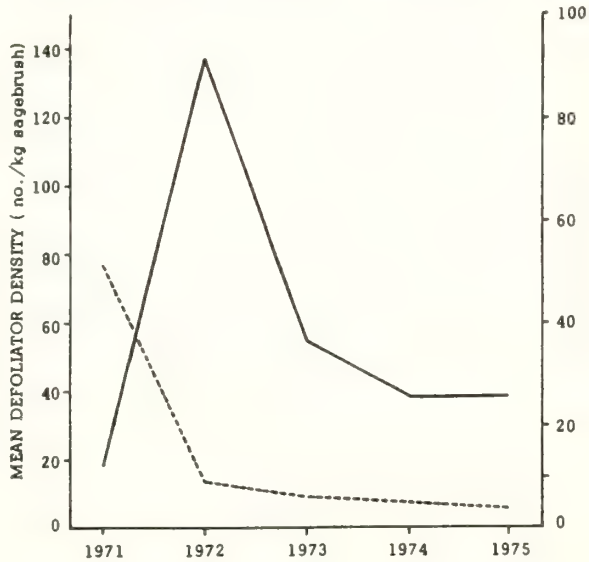

Figure 2.--Five-year population trends of the defoliator (solid line) and its parasitoids (dotted line) at Curlew Valley site.

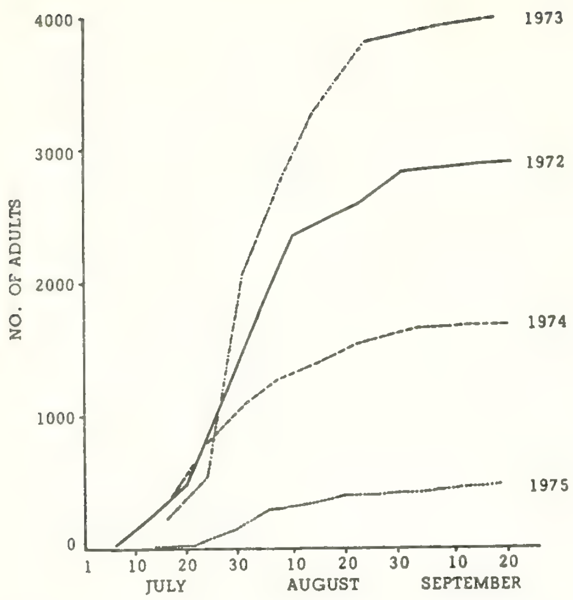

Figure 3.--Cumulative record of defoliator moths captured in a Malaise trap at Curlew Valley site during four seasons.

Intermountain region (Beetle 1960; Holmgren and Reveal 1966; McArthur and others 1979).

Two types of experiments were conducted to determine the host range of the defoliator. Laboratory tests determined the acceptability and suitability of 21 species and varieties of Artemisia and 15 other plant species (Hsiao and Green 1974). Ten field-collected fourth and early fifth instar defoliator larvae were group-reared in plastic cages on individually potted plants or fresh foliage. Foods were changed as needed. There were three to four replicates on each test plant. Percent survival, pupal weight, and rearing duration were criteria of acceptability and suitability. Several Artemisia species were obtained from the U. S. Department of Agriculture, Forest Service, Great Basin Experiment Station in Ephraim, UT. Other plants collected throughout Utah and southern Idaho were established in pots for rearing experiments.

None of the 13 tested Compositae plants outside the genus Artemisia were acceptable to the defoliator: Chrysothamnus viscidiflorus, C. nauseosus, Chaenactis douglasii, Tetradymia canescens, Townsendia scapigera, Senecio canus, Erigeron pumilus, Cirsium undulatum, Tragopogon dubius, Wyethia mulenburgia, Taraxacum officinale, Erigeron sp. (1), Erigeron sp. (2) (Hsiao and Green 1974). Two other plant species, Atriplex confertifolia (Chenopodiaceae) and Purshia tridentata (Rosaceae) were also unacceptable. All of these plants are commonly found in the habitats of Artemisia and can be excluded as potential hosts for the defoliator.

Among Artemisia, no feeding was observed in the following five species: A. abrotanum, A. absinthium, A. dracunculus, A. ludoviciana ssp incompta, and A. ludoviciana ssp ludoviciana. Slight feeding but no growth was found on seven species: A. cana ssp viscidula, A. carruthii, A. filifolia, A. frigida, A. longiloba, A. ludoviciana ssp candicans, and A. rothrockii. Successful rearings were recorded for nine species and varieties (table 2). Pupal weights and adult yields indicated that the six most suitable plants were A. arbuscula, A. bigelovii, A. cana ssp cana, A. tridentata ssp tridentata, A. tridentata ssp wyomingensis, and A. tripartita The three less suitable plants were A. nova, A. pygmaea, and A. spinescens. With the exception of A. spinescens, all acceptable plants were from the Artemisia subgenus Tridentatae (table 2) (McArthur and others 198

Oviposition preferences of the defoliator were tested in three field cages (3.3 by 5 by 6.6 f 1 by 1.5 by 2 m) (Hsiao and Green 1974). Each cage contained nine potted plants, one plant from each of eight Artemisia species and a plant from an unrelated Compositae. Newly emerged adults were released in the cages duri late July and early August. The potted plants were inspected for defoliator eggs during October. No eggs were found on A. caruthii, A. frigida, A. ludoviciana, and the gum-plant Grindelia squarrosa. Eggs were recovered fro all three caged plants of A. tridentata, from two of three plants of A. spinescens, and from one of three plants of A. arbuscula, A. bigelovii, and A. cana ssp viscidula. With the exception of A. cana ssp viscidula which received one egg, those species subject oviposition were also accepted by the larvae (table 2). Clearly, oviposition and feeding preferences of the defoliator are correlated with Artemisia species.

Field surveys of the host range of the defoliator were conducted throughout Utah in 1973 (Hsiao and Green 1974) and in southern Idaho in 1974 (Hsiao and Temte 1975). The following six Artemisia plants showed no evidence of defoliator infestation in Utah: A. bigelovii, A. carruthii, A. ludoviciana ssp candicans, A. ludoviciana ssp incompta, ludoviciana ssp ludoviciana, and A. pygmaea. However, both A. bigelovii and A. pygmaea were accepted as hosts during laboratory rea (table 2). Throughout Utah and southern Ida A. tridentata and A. tripartita were the mos important natural hosts of the defoliator. arbuscula was also infested but this species was less abundant and succulent than other species. Defoliator pupae collected from A. arbuscula were consistently smaller than tho from favorable hosts (Hsiao and Green 1974).

DEFOLIATOR IMPACTS ON BIG SAGEBRUSH

In 1973, a study was initiated at the Curle Valley site to assess the long-term effect the defoliator on sagebrush mortality and

Table 2.--Suitability of *Artemisia* species for the defoliator (Fourth and young fifth instar larvae were used in these tests)

Species	No. defoliator	Percent pupated	Mean pupal wt. mg ± S.E.	Percent yield of adult
A. arbuscula[1]	40	57.5	10.8 ± 0.33	30.0
A. bigelovii	40	32.5	8.9 ± 0.33	20.0
A. cana ssp *cana*	30	30.0	10.2 ± 1.07	16.7
A. nova[1]	30	23.3	7.8 ± 0.75	10.3
A. pygmaea	30	23.3	7.5 ± 0.49	3.3
A. spinescens	30	6.7	7.4 ± 1.90	3.3
A. tridentata ssp *tridentata*[1]	30	53.3	9.9 ± 0.48	26.7
A. tridentata ssp *wyomingensis*[1]	30	33.3	8.7 ± 0.84	20.0
A. tripartita[1]	30	23.3	9.6 ± 0.33	16.7

[1] Recorded natural hosts of the defoliator.

roductivity. During July, when defoliator eeding ceased, 150 completely defoliated agebrush plants were tagged at the study site. n September and October these plants were hecked to determine size (plant height and iameter) and status of growth (number of live ranches per plant, number and size of flower talks, etc.) The biomass (green and stem eights) of several defoliated plants was etermined to assess productivity. A group of ealthy sagebrush plants from the study site was valuated in the same manner to determine the ormal level of plant productivity under minimum nsect damage. All tagged plants were monitored gain in 1974, 1975, and 1976 to determine plant ortality due to defoliation.

second study conducted at the same site during 974 and 1975 determined how defoliator nfestations affected sagebrush productivity. t the beginning of the field season, about 40 ealthy sagebrush plants were treated with an nsecticide (Temik in 1974; Dieldrin in 1975) to stablish them as defoliator-free controls. In arly July of both years, when there was about) percent pupation of defoliators, 70 to 100 efoliated plants were tagged and examined to etermine levels of defoliator infestation; that s, numbers of feeding and webbing sites and efoliators. The height, crown dimensions, and umber of living and dead branches were also ecorded for each plant. In October, following he flowering and fall growth periods of the agebrush, the control plants and the tagged efoliated plants were measured again, cut off t the ground level, and taken to the laboratory here fresh and dry weights of the total plant, oliage, flowers, and woody parts were etermined. The number of flower stalks, flower talk length from basal to terminal flower, and he number of live and dead branches were ecorded for each plant. The insecticide-treated ontrol plants indicated normal levels of plant roductivity under minimum insect damage.

able 3 shows how defoliator infestation affected sagebrush productivity. A detailed statistical analysis of these data was presented by Temte (1977). In general, an increase in the number of defoliators was associated with a decrease in the number of flower stalks (the reproductive tissue of the plant). The number of flower stalks was also positively correlated with the weight of the plant, and may reflect the plant's age and reproductive potential. Foliage production also decreased as the number of defoliators increased. This was more apparent in 1975 than in 1974. Because defoliator infestations at the study site were relatively low during both years, the defoliators' overall impact on sagebrush productivity was not as apparent as it would have been at higher infestation levels.

By 1976, long-term effects of the defoliator on sagebrush were noticeable on tagged plants (Hsiao and Temte 1976). Of the 148 sagebrush plants tagged in July 1973, completed records over the four seasons were available on 123 plants. Of these, 82 plants (66.7 percent) survived. Sagebrush mortality was 18.7 percent in 1973 and 13.8 percent in 1974, but was insignificant thereafter as defoliator infestation decreased (figs. 2 and 3). The mean number of live branches per plant decreased by 40 percent in the fall of 1973, 50 percent in 1974, and stabilized at 57 percent in 1975. Only 43 percent of the total branches were alive at the end of the study period, an indication that there were fewer live branches on surviving plants. The number of plants that flowered each year also declined initially and gradually increased in subsequent years. Sagebrush mortality by plant height, presumably reflecting different age groups, is depicted in fig. 4. Mortality was over 50 percent for plants 16-24 inches (41-60 cm) high, about 25 percent for those 32-35 inches (81-90 cm) high, and over 40 percent among plants of 36-55 inches (91-140 cm) high. Thus, small and large plants were more vulnerable to defoliator damage.

Table 3.--Effects of defoliator infestation levels on sagebrush productivity

Level of infestation: No. defoliator per plant	No. plants examined	Mean No. defoliator per kg fresh sagebrush	Mean No. flower stalks per plant	Percent foliage weight	Percent dead branches	Mean plant height	Mean plant weight
						cm	kg
1974							
1-5	29	22.5	15.3	15.6	20.5	51.5	.194
6-10	27	57.5	11.3	14.3	6.5	50.5	.189
11-20	9	84.6	7.1	13.5	13.7	46.1	.251
Control	30	-	15.6	14.7	0.8	62.5	.281
1975							
1-5	35	29.8	14.5	22.2	6.7	49.5	.160
6-10	12	64.6	8.6	18.2	5.0	52.0	.171
11-20	14	82.8	23.1	18.5	7.7	56.3	.249
Control	24	-	63.7	25.6	0	67.3	.479

These data indicate that moderate defoliator infestation decreased sagebrush productivity by reducing the amount of foliage and the number of new flower stalks. Severe defoliator infestation could kill sagebrush branches or entire plants, especially when such an infestation continues for several years.

CONCLUSIONS

Sagebrushes, among the most common and important native plants of the arid Western United States, are found on an estimated 270.3 million acres (109.4 million ha) (Beetle 1960). Approximately 11 percent (6.2 million acres; 2.5 million ha) of Utah is dominated by various species of sagebrush (McArthur and others 1979). Throughout this region, the sagebrush defoliator is considered to be the most important insect pest. The defoliator is a restricted feeder that has evolved to feed on a few Artemisia species of the subgenus Tridentatae, species well-known for possessing a variety of allelochemicals, notably terpenoids and phenolics. Since only 3 of 18 indigenous species of the genus Aroga are known to feed on Artemisia (Busck 1939; Hodges 1974), their adaptation to these food plants is unique. The known host for Aroga rigidae is Artemisia rigida (Clarke 1936) and for A. eldorado is Artemisia vulgaris (Keifer 1936). These two Aroga species are not as common as A. websteri and little is known about their biology. The wide geographic distribution of the sagebrush defoliator in several western states and dramatic increases in infestation levels indicate that the species is well adapted to its environment.

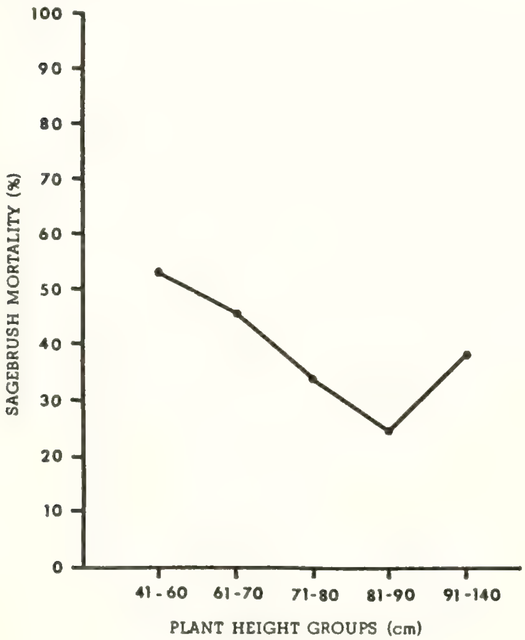

Figure 4.--Size-related mortality in severely defoliated big sagebrushes at Curlew Valley site after a 2-year period.

Both abiotic and biotic factors influenced the defoliator population at the Curlew Valley site. The defoliator has high reproductive potential. As a native insect, it also supports a wide range of natural enemies. About 20 species of parasitoids, predators and diseases have been recovered from the defoliator. However, natural enemies are not important in stabilizing the population in most years. Abiotic factors appear to be more important. Weather affects the defoliator population through the insect's host plants. Hot, dry periods cause water stress on the sagebrush plants and reduce moisture in the foliage, thus reducing foliage acceptability to the defoliator larvae, especially during their prime feeding period. These factors caused the population declines

observed in 1974 and 1975. Such density-independent factors have similar effects on the insect's natural enemies, since parasitism had little influence on defoliator numbers during this period. Periodic outbreaks of defoliators reported in several western states are probably due to favorable weather conditions during consecutive years. Monitoring weather conditions may provide a realistic method to predict defoliator population trends.

Several common sagebrushes provide food for the defoliator. Severe defoliator infestation can substantially reduce foliage and kill sagebrush plants. Plant loss due to defoliator infestation is a valid concern in range management. For reasons noted above, it does not appear feasible to manage the defoliator by manipulating its natural enemies. Other than conventional insecticides, the most promising strategy appears to be the selection and breeding of sagebrush varieties or species that are unacceptable to the defoliator. This strategy is feasible because of the high degree of host specificity of the defoliator. Screening for plant resistance to the defoliator may occur in conjunction with current attempts to select sagebrushes superior as animal feed. Failure to consider insect damage in plant breeding programs could result in sagebrushes that are more acceptable to the defoliator.

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RABBITBRUSH (CHRYSOTHAMNUS NAUSEOSUS SSP. CONSIMILIS)

MORTALITY ASSOCIATED WITH

DEFOLIATION BY A LEAF-FEEDING BEETLE, TRIRHABDA NITIDICOLLIS

Raymond S. Dalen, Reggie A. Fletcher, and Francis A. Winter

ABSTRACT: Defoliation of rabbitbrush (Chrysothamnus nauseosus (Pallas) Britt. ssp. consimilis (Greene) H. & C.) by a leaf-feeding beetle (Trirhabda nitidicollis LeConte (Coleoptera: Chrysomelidae)) on herbicide-treated and untreated plants on 10 paired transects in the Zuni Mountains of New Mexico was monitored from 1978 to 1983. While 2,4-D and picloram treatments were generally ineffective in controlling rabbitbrush, they did not appear to affect leaf beetle defoliation. Plant mortality varied by transect from 7 to 68 percent. Mortality relates well to small plant height and 2 consecutive years of heavy or moderate beetle defoliation. The leaf beetle is partially effective as a natural control for rabbitbrush.

INTRODUCTION

Rabbitbrush (Chrysothamnus nauseosus and C. viscidiflorus) covers 2,822,800 acres (1 142 834 ha) of rangeland in New Mexico in moderate or dense stands (Garrison and McDaniel 1982). Under favorable conditions, C. nauseosus spreads rapidly from light, prolifically produced, wind-disseminated achenes (McArthur and others 1979). Chrysothamnus nauseosus ssp. consimilis is a difficult plant to control and frequently invades the deeper soils adjacent to drainage bottoms at densities that compete with other forage species. In May 1978, a relatively heavy but spotty infestation of larvae of a leaf-feeding beetle (Trirhabda nitidicollis) was observed on rabbitbrush. Massey and Pierce (1960) had reported a relatively heavy infestation of this insect near the survey area in 1957, where large areas of rabbitbrush were killed. They suggested studies were needed to determine the possibility of using the insect as a biological control agent. Andres (1971) suggests there is a potential for the use of native insects in controlling native weeds.

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This paper reports the results of observation and demonstration plots established to determine the growth pattern and phenology of rabbitbrush and to monitor the effect of larval leaf beetle defoliation of rabbitbrush on herbicide-treated and untreated plants in west-central New Mexico.

On May 17, 1978, from the leaf beetle larval activity observed, we did not know if foliar-applied herbicides would be effective on insect-defoliated rabbitbrush. We also did not know the effects of combining herbicides with leaf beetle activity or how leaf beetle activity would be affected by herbicides.

LEAF-FEEDING BEETLE PHYSIOLOGY

The leaf beetle occurs from western Montana to New Mexico, westward to southern California (Hogue 1970). The adult beetle is 0.5 to 0.75 inches (13 to 19 mm) long with a yellowish-green stripe in the center and on each side of the elytra. The pronotum is yellow, with three blue-green spots, one located in the center and one on each side (Massey and Pierce 1960).

Hogue (1970) described the leaf beetle life cycle. Emergence from the egg coincides with the development of new leaf growth on the host plant in the spring. The small (1 to 2 mm) shiny, black first instar larvae crawl up the main stem and lateral branches of the host plant to the terminal foliage where feeding begins. Second larval instars are sedentary and feed primarily at the base of new leaf fascicles. By the fourth instar, the large (7 to 12 mm) larvae are very active. Prepupal larvae burrow into the soil at the base of the host plant to a depth of 0.25 to 0.5 inch (6 to 13 mm), where a pupal chamber is formed. The pupal period is approximately 10 days. After emergence, adults feed on the host plants for 6 to 8 days before mating. Fifteen to 20 days after mating, the female deposits her eggs in the soil at the base of the host plant, where they overwinter.

Hogue (1970) did not measure the effects of larvae and adults on host plants, but stated that beetle populations may increase rapidly and defoliate host plants resulting in reduced vigor or death. During the initial stages of an infestation, distribution of the leaf beetle in the rabbitbrush community is uneven. Adults and/or larvae may be present in large numbers on some plants but absent from other plants. At the peak of an infestation, nearly all plants are heavily infested. Massey

and Pierce (1960) observed larval feeding only on rubber rabbitbrush (C. nauseosus), but adults were found feeding on rubber rabbitbrush and big sagebrush (Artemisia tridentata). Utilization by the adults was not heavy enough to cause damage. Hogue (1970) reported host plants of the leaf beetle as two species of rabbitbrush, C. nauseosus and C. viscidiflorus, and Acamptopappus sphaerocephalus.

MATERIAL AND METHODS

The monitoring of leaf beetle defoliation on rabbitbrush was conducted in the Zuni-Bonita Canyon area of the Zuni Mountains located in the Cibola National Forest. The site is about 10 miles (16 km) southwest of Grants, Cibola County, NM. Average elevation is 7,500 ft (2 286 m). Average annual precipitation is 16 inches (40.6 cm), 40 percent of which occurs during the summer period of May-September. Rabbitbrush is the primary overstory in the open canyon bottoms. Elsewhere, ponderosa pine (Pinus ponderosa) dominates all but the most exposed slopes where pinyon pine (Pinus edulis) dominates. The soils are deep, well drained, and high in inherent fertility. They are Typic Argiborolls and Cumulic Haploborolls. The most common grass species are blue grama (Bouteloua gracilis) and western wheatgrass (Agropyron smithii). Livestock grazed the study area from 1978 to 1981, but were not present in 1982 and 1983.

The monitored rabbitbrush plants were located on 10 paired belt transects 4.36 by 100 ft (1.33 by 30.5 m) established on July 10-11, 1978, in rabbitbrush-invaded canyon bottoms. Eight transects were in Zuni Canyon in an area of about 320 acres (129 ha). Two transects were about 2.5 miles (4 km) south in Bonita Canyon. The transects were located in areas subjectively assessed as having light, moderate, and heavy leaf beetle defoliation based on general observations during the May 1978 survey. Light defoliation sites were represented by transects 5, 6, 7, and 8; moderate defoliation sites included transects 3 and 4; moderate to heavy, transects 1 and 2; and heavy defoliation by transects 9 and 10. The classification of light, moderate, and heavy defoliation based on transect means is 0-34, 35-74, and 75-100 percent.

The location of each rabbitbrush plant rooted within the transect was recorded along a center-line reference tape. The transects were measured each July from 1978 to 1983. Each rabbitbrush plant was measured as follows: (1) live crown height (initially measured to the nearest foot (0.3 m), but from 1980 on, small plants 0.5 feet (0.15 m) or less were also recorded); (2) live crown, visually estimated to the nearest 10 percent; (3) live crown defoliated, visually estimated to the nearest 10 percent; and (4) presence or absence of adult beetles.

On July 19, 1978, two 1-acre (0.45-ha) plots in Zuni Canyon that included two transects in lightly defoliated areas were treated with herbicides using a ground sprayer with a 20-ft (6.1-m) spray boom. A mixture of triisopropanoline salts at the rate of 1 lb/acre (1.12 kg/ha) acid equivalent (ae) 2,4-D and 0.25 lb/acre (0.28 kg/ha) ae picloram was applied to the plot that included transect 5, and 2 lb/acre (2.24 kg/ha) ae 2,4-D and 0.5 lb/acre (0.56 kg/ha) ae picloram to the plot that included transect 6, both in 19.5 gal/acre (182 L/ha) of water.

On July 24, 1978, a 5-acre (2.27-ha) plot in Zuni Canyon that included transect 1 was treated with 3 lb/acre (3.36 kg/ha) ae of 2,4-D ester (propylene glycol butyl ether) in 19.25 gal/acre (180 L/ha) of water with the same ground sprayer.

On April 13, 1979, just before bud break, 3 lb/acre (3.36 kg/ha) ae of 2,4-D ester in a diesel oil carrier at 12 gal/acre (112 L/ha) was applied to two sets of 20- by 33-ft (6.1- by 10.1-m) plots each replicated three times. The herbicide was applied using a 5-ft (1.5-m) hand-held spray boom. One set of plots was located near transects 5, 6, 7, and 8 representing light leaf beetle infestation and light defoliation. A second set of plots was located near transects 9 and 10 representing heavy leaf beetle infestation and heavy defoliation. The treated plots, and paired number of untreated plots, were sampled on August 18, 1979, July 8, 1980, July 31, 1981, and August 5, 1983. The same measurements as gathered on the 10 transects were recorded.

Four transects were sampled on October 3, 1979, and six transects on November 5, 1980, to determine the amount of flower development. Flower development on each plant was visually estimated as none, light, moderate, and heavy. Heavy meant that flowers were present over the total plant crown.

Rabbitbrush mortality on the 10 transects is the net percentage accumulated plant loss based on the number of live plants measured in July 1978. Plants recorded as dead occasionally resprouted the following year.

Statistical analysis of the data is limited since the 10 belt transects represent observation plots and were not replicated. The transect mean percentage defoliation is the mean of all the live plants. The standard deviation and variance was calculated and the "t" test was used to determine the significance of the difference in mean percentage defoliation each year on the same transect.

A stepwise logistic regression was used to predic rabbitbrush survival or mortality (Dixson and others 1981). Independent variables were mean percentage defoliation for the two highest consecutive years and mean live plant height the same two years during the period 1978 to 1982. Since two consecutive years of individual plant data were used, survival or mortality was for the period 1980 to 1983. Plants that died in 1979 an new plants were not included. The logistic model is fitted directly to actual values measured for 369 individual plants from the untreated transects.

SULTS AND DISCUSSION

ansects

e life cycle of the leaf beetle coincides with e growth pattern of rabbitbrush (fig. 1). The aviest defoliation occurs from larval feeding on bbitbrush during its slow growth period. After e emergence of adults, the plant may resprout d recover except when the defoliation is heavy ough to result in reduced vigor; this restricts th resprouting and flower development. The ming shown in figure 1 varies slightly with nual climatic conditions.

e larvae fed on all height classes of plants. r example, in 1978, the mean defoliation of ants in the 1-, 2-, and 3-ft height classes was , 63, and 57 percent, respectively. Defoliation plants in the 4- and 5-ft height classes was 46 d 35 percent, but the number of plants sampled s small. This agrees with Massey and Pierce 960) who reported larvae fed on plants of all es.

me leaf beetle defoliation occurred on each ansect every year, except on transect 4 in 82. The overall level of leaf beetle activity sed on mean percent defoliation peaked in 1979 6 of the 10 transects (table 1). Activity on ansect 1 did not peak until 1983, while that on ansects 3, 9, and 10 peaked in 1978. The mean rcentage defoliation combining all transects was ghest in 1979 at 74 percent, but was at its west point at 13 percent the next year (ble 1). Leaf beetle activity was not uniform roughout the study area. Small areas of heavy oliation were interspersed with areas of light ivity. The mean percentage defoliation on four the 10 transects was significantly different ing each of the 5 years (table 1). Moderate oliation occurred on at least one transect 5 of 6 years. Heavy defoliation occurred 3 of the ears on at least two transects. No transect heavily defoliated 2 consecutive years, but r transects had 2 consecutive years of heavy moderate defoliation. Three other transects e moderately defoliated for 2 consecutive rs.

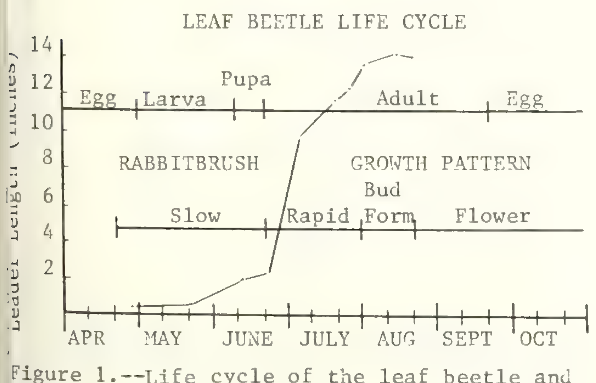


Figure 1.--Life cycle of the leaf beetle and growth pattern and phenology of rabbitbrush. Leader length (inches) 1979.

Table 1.--Mean percentage defoliation of rabbitbrush plants by the leaf beetle, July sample each year, by transect and treatment

Transect	Treatment	1978	1979	1980	1981	1982	1983
		Percent[1]					
1	2,4-D[2]	62	52	34	62*	60	83
2	None	44	96*	8*	27*	14*	59*
3	None	92	8*	47*	71*	2*	6
4	None	28	95*	4*	53*	0*	3*
5	2,4-D+picloram[3]	32	97*	4*	46*	75*	28*
6	2,4-D+picloram[4]	22	92*	23*	39	52	56
7	None	29	56*	21*	22	30	47*
8	None	26	78*	15*	40*	32	47
9	None	82	65*	5*	16*	34*	39
10	None	91	73*	2*	5*	58*	81*
	No treatment mean	63	73	12	29	28	45
	Treatment mean	41	82	18	50	66	50
	Mean	60	74	13	33	35	46

[1]Means with an asterisk are different from the preceding year at the 5 percent level using the t test.

[2]Three lb/acre (3.36 kg/ha) ae 2,4-D PGBE ester, July 24, 1978.

[3]One lb/acre (1.12 kg/ha) 2,4-D ae + 0.25 lb/acre (0.28 kg/ha) picloram ae both triisopropanoline salt.

[4]Two lb/acre (2.24 kg/ha) 2,4-D ae + 0.5 lb/acre (0.56 kg/ha) picloram ae, both triisopropanoline salt.

Untreated transects.--The shifting beetle activity is also evident based on individual plant data. Only two of 417 plants located on the untreated transects were heavily defoliated 3 consecutive years during the study period. A total of 100 plants (24 percent) were heavily defoliated, with 65 of these completely defoliated 2 consecutive years. A total of 247 plants (59 percent) were heavily defoliated at least 1 year.

Sixty-three of the 65 rabbitbrush plants on the untreated transects were completely defoliated in both 1978 and 1979. This was followed by 2 years of light defoliation, allowing the remaining live plants to recover. Of these 63 plants, mortality peaked at 52 percent in 1981, remaining relatively constant through 1983 (fig. 2).

Adult leaf beetle activity appears to be more consistent than larval activity. The frequency of plants with adult leaf beetles varied from 23 to 50 percent during the study period and was about average (37 percent) in 1980, the year with the lowest mean percent defoliation.

Rabbitbrush mortality over the 5-year period by transect is shown in table 2. Mortality of plants on the untreated transects was 51 percent by 1981 and increased slightly to 54 percent by 1983. Natural senescence or loss due to other factors could not be determined or isolated, but the mortality in 1981 is primarily attributed to leaf beetle defoliation in 1978 and 1979. The transects with the highest plant mortality generally had the highest mean percent defoliation during 2 consecutive years and the lowest mean live plant height the same 2 years. One year of heavy defoliation is apparently less effective. The heavy defoliation on transect 4 in 1979, between 2 years of light defoliation, resulted in 29 percent plant loss in 1981 (tables 1 and 2). On transect 10, 2 consecutive years with heavy and moderate defoliation in 1978 and 1979 resulted in 62 percent plant loss in 1981 (tables 1 and 2). The mean live plant height for the 1978-79 period was 1.3 ft (0.4 m) in both transects 4 and 10.

The stepwise logistic regression (Dixson and others 1981) suggests a relationship of rabbitbrush mortality to defoliation and plant height (fig. 3). The percent probability of mortality increases as mean percent defoliation increases over 2 consecutive years and as live plant height decreased the same 2 years. Individual plant data, when used to predict rabbitbrush survival or mortality, are predictable only 60 percent of the time. Also, the regression predicts some mortality for all plant height

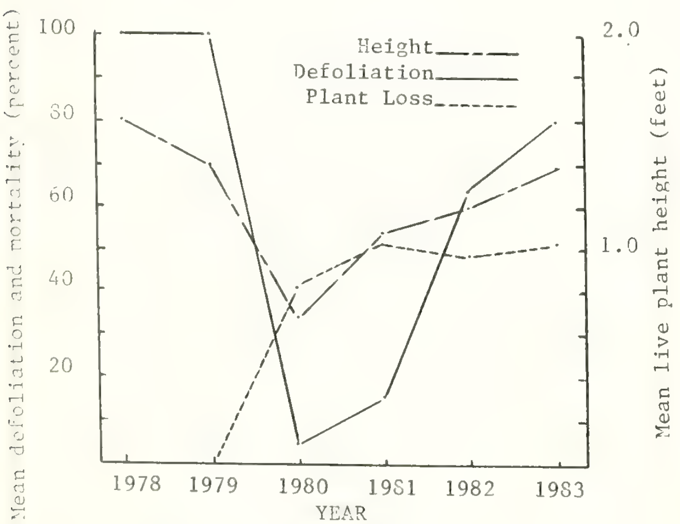


Figure 2.--Yearly mean percentage defoliation, percentage plant mortality, and mean live plant height of 63 rabbitbrush plants on the untreated transects completely defoliated by the leaf beetle in both 1973 and 1979.

Table 2.--Percentage plant mortality 1978 to 1983, using number (N) of live plants 1978 as baseline, rabbitbrush, July samples

Transect	Live Plants, 1978	1978	1979	1980	1981	1982	1983
	N	Percent[2]					
[1] 1	29	0	21	31	38	38	45
2	119	0	24	59	67	64	66
3	32	0	0	3	19	31	31
4	35	0	9	9	29	29	34
[1] 5	28	0	4	0	0	0	7
[1] 6	19	0	5	21	47	47	47
7	23	0	0	0	17	22	13
8	26	0	8	15	19	19	27
9	79	0	14	33	54	51	56
10	103	0	25	52	62	60	68
Untreated	417	0	17	38	51	50	54
Treated	76	0	11	17	26	26	3[illegible]

[1]Herbicide treated transects, see table 1.

[2]Sixty new plants that came in on the untreated transects and one new plant on the treated transects are not included.

classes with no defoliation, indicating there are additional variables, such as age and plant competition, which were not measured.

Moderate and heavy defoliation appear to reduce plant vigor and flower development. For example, on transect 4 in July 1979, the mean defoliation was 95 percent; only 3 percent of the plants developed flowers that year. In 1980, mean defoliation decreased to 4 percent and 25 percent of the plants developed flowers. On transect 10, which was heavily and moderately defoliated in 1978 and 1979, only 1 percent of the plants developed flowers in 1979. Defoliation was ligh in 1980, but only 8 percent developed flowers indicating the plants apparently had not recovered. On transect 2, which received moderate, heavy, and light defoliation in 1978, 1979, and 1980, respectively, 47 percent of the plants developed flowers in 1980. Flower development also appeared to be greater with increased mean plant height.

Treated transects.--The general trend in mean percentage defoliation on the treated transects was similar to that on untreated transects (table 1). The shifting beetle activity was als similar. Only three plants were heavily defoliated 3 consecutive years during the study period. A total of 17 plants (22 percent) were heavily defoliated with seven completely

foliated for 2 consecutive years. A total of plants (62 percent) were heavily defoliated at ast 1 year.

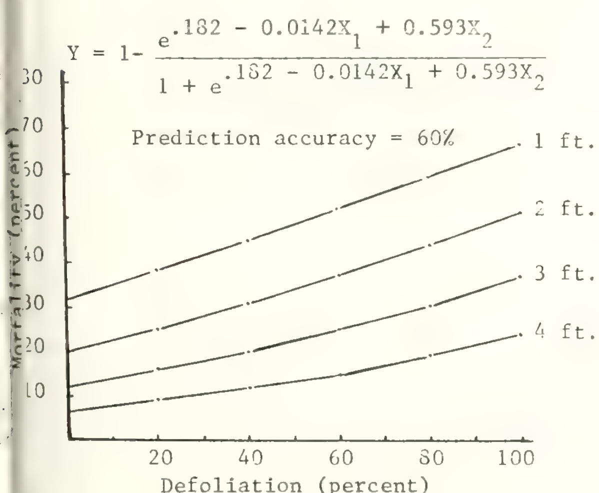
rbicide treatments during July 1978 had no parent effect on leaf beetle defoliation tivity in 1979. Mean defoliation on transect 1 creased from 62 to 52 percent, but the fference in the means is not significant. On ansects 5 and 6, defoliation increased from ght to heavy (table 1).

e effectiveness of herbicide treatment alone in ntrolling rabbitbrush cannot be determined rectly. By July 1981, no mortality was recorded transect 5, but the higher rate of 2,4-D and cloram applied to transect 6 resulted in 47 rcent mortality (table 2). The logistic gression equation (fig. 3) indicates that pected plant mortality on transect 6 without rbicide treatment would have been 28 percent. is suggests the herbicide treatment on this ansect resulted in more plant mortality than edicted from defoliation alone.

e 2,4-D treatment on transect 1 was not fective in killing rabbitbrush. The 45 percent ant mortality recorded in July 1983 (table 2) is milar to the 45 percent predicted plant loss th defoliation alone using the logistic gression (fig. 3).

e moderate defoliation of plants on transect 1 d light defoliation in 1978 on transects 5 and 6 y have affected herbicide results.

e frequency of plants with adult leaf beetles ried from 55 to 83 percent during the study riod and was about average (65 percent) in 1980, e year with the lowest mean percent defoliation.



gure 3.--Probability of percentage mortality (Y) rabbitbrush 1980-83 from mean percentage foliation (X_1) over the 2 highest consecutive ars and mean live plant height in feet (X_2) the me 2 years during the period 1978-82. Based 369 individual plants from the untreated ansects using stepwise logistic regression.

Table 3.--Mean percentage defoliation by the leaf beetle and percent mortality of rabbitbrush following dormant spray treatment with an ester of 2,4-D in diesel oil, April 13, 1979, on light and heavy defoliation classes at two sites

Defoliation class and treatment		Date Sampled			
		8/17/79	7/08/80	7/31/81	8/05/83
		Percent defoliation[1]			
Light					
Treated		85	15*	14	13
Control		67	31*	35	6*
Heavy					
Treated		100	0*	24*	83*
Control		100	7*	32*	68*
	N[2]	Percent mortality[2]			
Light					
Treated	44	2	9	5	2
Control	32	0	3	6	16
Heavy					
Treated	47	26	66	81	79
Control	46	15	50	67	72

[1]Defoliation means with an asterisk are different from the preceding year at the 5 percent level using the t test.

[2]Plant mortality is based on the number (N) of plants measured 8/17/79 and does not include three new plants which came in.

Dormant Spray Plots

The dormant herbicide treatment did not appear to be effective in killing rabbitbrush at either the light- or heavy-defoliation sites. The percentage plant mortality in 1983 was much higher on the heavy-defoliation site compared to the light-defoliation site, but the treated and control plots at both sites had similar mortality (table 3). The treatment did not seem to inhibit leaf beetle defoliation.

The treated and control plots at the light defoliation site were heavy and moderately defoliated in 1979. This was not expected but was consistent with the heavier defoliation measured on transects 5, 6, 7, and 8 (tables 1 and 3). The heavy-defoliation site was heavily defoliated in 1979, and the trend in 1980, 1981, and 1983, was consistent with the defoliation measured on transects 9 and 10 (tables 1 and 3).

CONCLUSIONS

Results from this preliminary study where defoliation of rabbitbrush was monitored on 10 transects and the dormant spray plots suggest the leaf beetle is at least moderately effective as a natural control of rabbitbrush.

In this study, herbicide treatments did not increase rabbitbrush mortality when coupled with leaf beetle defoliation. Transect 6, where the higher rate of 2,4-D and picloram was applied, may be an exception. However, herbicide treatments did not appear to inhibit leaf beetle defoliation.

Even a moderate reduction of rabbitbrush in dense stands or stabilization of density in light or moderate stands is beneficial. Total elimination of rabbitbrush is not needed. In habitats with scattered plants, this species has little effect on herbaceous species and on some sites it does not suppress grass growth (McArthur and others 1979).

The effects of grass competition on rabbitbrush mortality and reduced seedling establishment were not measured, but observations in 1983 and July 1984 suggest that western wheatgrass is more competitive than blue grama. Further studies should assess the effectiveness of grass competition in conjunction with leaf beetle defoliation.

Research is needed to determine how leaf beetle populations can be modified, introduced, or enhanced, and information is needed on population dynamics, parasitism, and predation. Additional work is also needed on the interaction of leaf beetles and more effective herbicides in reducing rabbitbrush stands.

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SPECIFICITY OF GALLS ON *CHRYSOTHAMNUS NAUSEOSUS* SUBSPECIES

E. Durant McArthur

ABSTRACT: Several galls of distinctive morphology occur on rubber rabbitbrush (*Chrysothamnus nauseosus*). "Cotton" and "callus" galls are induced by tephritid flies (Diptera: Tephritidae) of the genus *Aciurina*. "Mace" and "flower" galls are induced by other insect species. Evidence from several sites in Utah and Arizona over a 10-year period indicates that tephritid taxa ("sibling species") partition the *Chrysothamnus* resource differently in different areas. Different tephritid taxa cause different gall forms; tephritid populations fluctuate over time, and there is a relationship between gall forms and rubber rabbitbrush taxonomy. Callus galls are found only on the white-stemmed *C. nauseosus* ssp. *albicaulis* and ssp. *hololeucus* at my study sites. Cotton galls are commonly found on the green-stemmed subspecies *C. nauseosus* ssp. *consimilis*, *turbinatus*, and *graveolens*. Flower and mace galls show less plant and host specificity. Sibling species formation of *Aciurina* spp. may be facilitated by changes in larval survival and host recognition genes.

INTRODUCTION

In an earlier paper, I and my colleagues made a case for gall form specificity on rubber rabbitbrush (*Chrysothamnus nauseosus*) subspecies (McArthur and others 1979b). In that paper we demonstrated that specificity of "cotton" and "callus" stem galls occurs at many locations in the central portion of the range of *C. nauseosus*. However, we acknowledged that in some locations the specificity was lacking. Wangberg (1976, 1978, 1980, 1981) also reported on varying degrees of gall form specificity in *Chrysothamnus* depending upon gall form and plant distribution. Wangberg's analyses were not confined to the cotton and callus galls, but covered a wide range of gall forms induced by three fruit fly genera (Tephritidae) on several *Chrysothamnus* species. Wangberg (1976, 1981) and McArthur and others (1979b) suggested that the flies (*Aciurina* spp.) that induce formation of cotton and callus galls show specificity in areas of fly sympatry and *C. nauseosus* ssp. sympatry and thus reduce interspecific competition by partitioning a resource.

In this paper, I report additional data on the specificity of gall forms now covering a 10-year period of observation. These data then are used in a plant/insect coevolutionary discussion.

SITES, MATERIAL, AND METHODS

Sites

I made observations of galls on *C. nauseosus* over a wide portion of the Intermountain area (Sierra Nevada to Rocky Mountains, 36° to 40° N. latitude) from 1975 to 1984. Many of these observations were incidental to other plant and data collection missions. However, I collected quantitative data on gall frequency at several Utah and Arizona sites during the period of study (Arizona: Mohave County, Moccasin. Utah: Iron County near Paragonah; Juab County near Nephi; Sevier County, Big Rock Candy Mountain; Sanpete County, Ephraim Canyon, near Fountain Green; Utah County near Goshen, Provo; Washington County, Gould Wash, near St. George).

Materials

Chrysothamnus nauseosus subspecies and other *Chrysothamnus* taxa were determined following the keys of Anderson (1973) and McArthur and others (1979a). *Chrysothamnus nauseosus* subspecific identification at some locations in the earlier report (McArthur and others 1979b) was corrected. The green subspecies at the Goshen Dam Site is ssp. *turbinatus*. The white subspecies at Paragonah, Fountain Green, and Gould Wash is ssp. *hololeucus*. Subspecies *hololeucus* and *albicaulis* are very similar, differing only in cryptic floral characteristics.

I observed many gall forms as described by Wangberg (1978, 1980, 1981) and Larew and Capizzi (1983). This paper emphasizes callus and cotton galls described and illustrated in McArthur and others (1979a, 1979b).

Callus gall: more or less glabrous, round to ovoid, 0.3-1.2 cm in diameter, and persistent up to 2 years.

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Cotton gall: covered with a thick white tomentum, round to ovoid, 0.7-1.4 cm in diameter, and generally not as persistent as the callus gall, although some persist for 2 years; the tomentum not as persistent as the gall body.

Cotton and callus galls are emphasized because they are locally and, I believe, geographically more widespread and abundant than the other galls. In addition, they are visually striking and prominent. Two other galls are also treated in a limited way. These are the "mace" gall of McArthur and others (1979b) and a gall that resembles a flower head gone to seed that I have designated the "flower" gall.

Mace gall: Usually glabrous, round to ovoid, 0.5-1.2 cm in diameter, and covered with small bracts. Persistence past the first year is unknown (see McArthur and others 1979b; Larew and Capizzi 1983).

Flower gall: Round to ovoid, 0.7-1.5 cm in diameter, subtended by several (4-8) more or less glabrous bracts (to 3.0 cm long), but "flower head" portion covered with cottony thick white tomentum. Persistence past the first year is unknown (see Larew and Capizzi 1983).

Emergent flies were collected from sample galls that had been brought into the laboratory and isolated in glass jars covered with cheesecloth. Flies were compared to the descriptions listed in Foote and Blanc (1963). J. K. Wangberg examined some of our fly specimens.

Methods

Gall frequencies were assessed in two ways. In one method, gall frequencies were scored in the manner that we used earlier (McArthur and others 1979b). Galls were counted on terminal 6 inches (15 cm) of a randomly selected branch of each mature shrub (>30 cm or >12 inches tall) on more or less straight line transects through Chrysothamnus populations. In a few cases, when gall frequencies were low, galls from the whole plant were counted. Fifty or more plants for each taxa were scored at each location as the plants occurred on the transects. The second way was to map out populations by scoring all plants for number and type of galls present. This technique was used at the Paragonah site where a ca. 50 by 300-ft (15-m by 275-m) transect was used to sample the populations and at Gould Wash where all plants were sampled along three transects totaling 3,400 ft (1 035 m) in length.

A paired t-test was used to test the significance of gall form frequency differences where two gall types occurred on the same rabbitbrush taxon (Woolf 1968).

RESULTS AND DISCUSSION

Gall Form Specificity

Plant galls may be restricted to a greater or lesser extent to various host plants (Mani 1964; Coulson and Witter 1984). An insect vector often produces a characteristic gall on a certain part of a specific plant. A problem with the specificity of gall forms on C. nauseosus is that species' proliferation of subspecies--some of which are similar and show some intergradation (Hanks and others 1975; Anderson 1984). We raised another possible point of confusion in our earlier paper stating that "another possible explanation for gall-form specificity is that different gall forms are not a response to different fly species, but rather a response to the host plant" (McArthur and others 1979b).

In the earlier paper (McArthur and others 1979b), we presented data from six C. nauseosus populations consisting of uniform subspecies bearing exclusively only cotton or callus galls. In those pure stands only cotton galls were found on ssp. consimilis and ssp. graveolens and only callus galls on ssp. albicaulis. A few other gall forms (e.g., mace galls) were also present. Results from the present study (tables 1 and 2, figs. 1 and 2, and observations) lead me to strengthen some points made in our earlier paper (McArthur and others 1979b) and draw some conclusions.

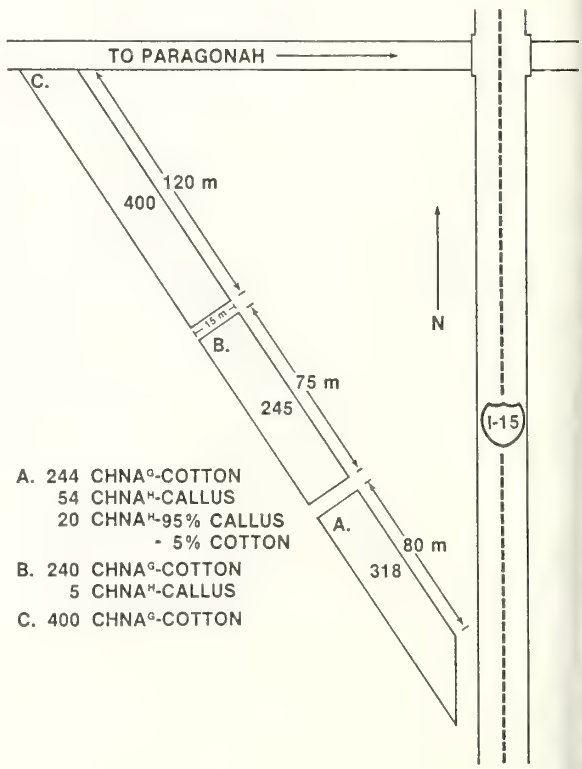

Figure 1.--Map of linear transect through Chrysothamnus nauseosus populations showing ssp. hololeucus ($CHNA^h$) and ssp. graveolens ($CHNA^g$), and gall form distributions near Paragonah, UT; 1980.

le 1.--Gall frequencies in Chrysothamnus populations, 1984

lection, location number, and taxon[2]	Gall type and frequency[1]		
	Callus	Cotton	Mace
hen Dam, Utah Co., UT			
hna^{h}, 1407[3]	0.34 ± 0.13 (0-5)	0	0
hna^{t}, 1408	0	8.92 ± 0.74 (0-34)	0
ld Wash, Washington Co., UT			
hna^{h}, 1526	8.92 ± 0.74 (0-28)	0	Rare[4]
hna^{g}, 1527	0	3.00 ± 0.32 (0-8)	Rare
casin, Mohave Co., AZ			
hna^{h}, 1410	0	2.66 ± 0.34 (0-6)	Rare
hna^{t}, 1409	0	10.42 ± 0.84 (0-24)[5]	0.38 ± 0.15 (0-9)
hvi^{v}, 1411	0	0	0.62 ± 0.21 (0-2)

e Sites, Materials, and Methods section; values are means ± standard error of the mean and in rentheses extreme range values.
breviations for Chrysothamnus taxa: Chna^{c} = C. nauseosus ssp. consimilis, Chna^{g} = C. nauseosus ssp. aveolens, Chna^{h} = C. nauseosus ssp. hololeucus, Chna^{t} = C. nauseosus ssp. turbinatus, Chvi^{v} = C. sciciflorus ssp. viscidiflorus.
thor's collection number.
served in population, but not necessarily on samples.
tton and mace frequencies significantly different (P <0.01).

le 2.--Gall frequencies at the Chrysothamnus nauseosus ssp. consimilis and ssp. hololeucus cline site; Parowan, UT; 1984[1]

ysothamnus population ucture and collection number	Gall type and frequency[2]			
	Callus	Cotton	Mace	Flower
form Chna^{h}, 1400[3]	4.80 ± 0.58 (0-24)	0	Rare (0-1)	Rare (0-4)
ed Chna^{h}, 1401	11.46 ± 1.00[4] (1-38)	0.08 ± 0.03 (0-1)	0.05 ± 0.05 (0-3)	0
Chna^{g}, 1402	0	7.18 ± 0.43[5] (1-16)	0.26 ± 0.10 (0-3)	Rare (0-1)
iform Chna^{g}, 1403	0	9.68 ± 0.56[5] (1-19)	0.18 ± 0.12 (0-6)	0

S figure 1 and Sites and Methods Section.
S Sites, Materials, and Methods section. Values are means ± standard error of the mean; numbers in prentheses are range values. Rare infers present in population, but only encountered on one or two sples.
Areviations for Chrysothamnus nauseosus ssp.: Chna^{h} = ssp. hololeucus, Chna^{g} = ssp. graveolens.
Cllus gall frequency significantly different than cotton and mace gall frequencies (P <0.01).
Cton gall frequency significantly different than mace gall frequency (P <0.01).

ist, in pure stands of subspecies within areas f general subspecies sympatry and high a-former populations, the gall forms maintain ight correlation to the C. nauseosus uspecies. In much of Utah the cotton gall is od exclusively on the green-stemmed uspecies consimilis, graveolens, and uinatus and the callus gall exclusively on h white-stemmed subspecies albicaulis and oleucus. In other areas, where one or the tr gall form is absent, a gall will sometimes pear on the nontypical host (McArthur and trs 1979b; Wangberg 1981). In this icussion, the rarer stem gall forms (mace, flower, and some illustrated by Wangberg [1978, 1980, 1981] and Larew and Cappizi [1983]) were not considered.

Second, in mixed or interdigitating stands of subspecies where both cotton and callus gall forms occur there is remarkable specificity. Cotton galls occur on the green-stemmed subspecies consimilis, graveolens, and turbinatus and callus galls on the white-stemmed subspecies albicaulis and hololeucus (McArthur and others 1979b; tables 1, 2). At two sites we did rather intensive sampling (figs. 1, 2). At a site in Iron County, UT, we sampled a uniform

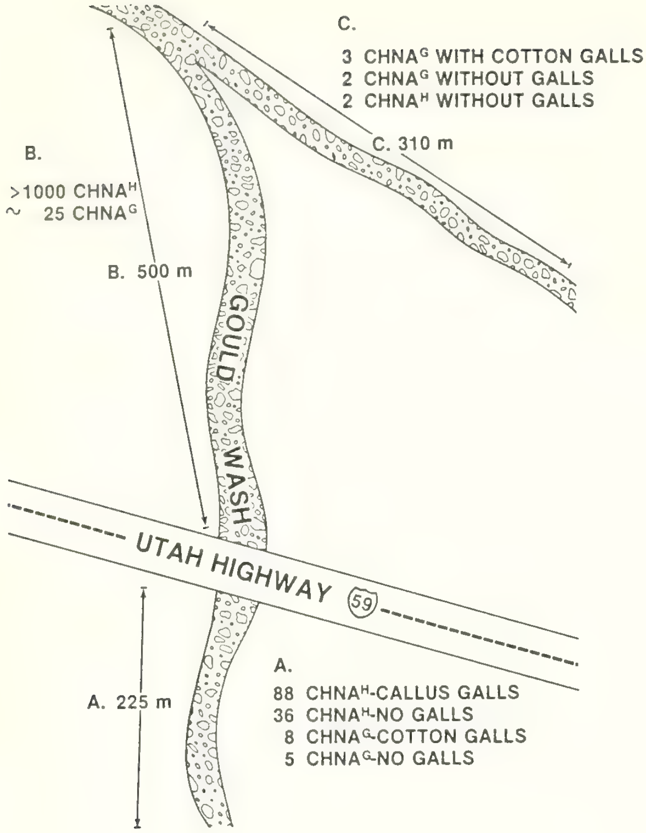

Figure 2.--Map of distribution Chrysothamnus nauseosus subspecies and gall form distributions in Gould Wash, UT, flood plain, 1980. C. nauseosus ssp. hololeucus (CHNA^{h}) in B segment have callus galls at relatively low frequency; C. nauseosus ssp. graveolens (CHNA^{g}) plants there are without galls.

ssp. hololeucus site in an abandoned field on the outskirts of Parowan and a mixed population grading into a pure stand of ssp. graveolens 2.5 mi (4 km) north, just west of Paragonah (table 2). Here the uniform ssp. hololeucus stand possessed callus galls only, and the uniform ssp. graveolens stand had cotton galls only. In the mixed stand, ssp. graveolens had cotton galls only; however, ssp. hololeucus had both kinds, but 97 percent of its sampled galls were callus (table 2).

At the site west of Paragonah, we inventoried 963 plants in 1980 (fig. 1). The results were similar to those given in table 2. Gall occurrence has been particularly heavy at that site. For example, in 1980 a large, 4.9 ft (1.5 m) tall by 6.9 ft (2.1 m) crown ssp. graveolens bush had 1,562 cotton galls and a large ssp. hololeucus, 4.3 ft (1.3 m) tall by 5.6 ft (1.7 m) crown bush had 262 callus galls and one cotton gall. A second intensive sampling was at the U-59 crossing of Gould Wash. At this site, callus galls and cotton galls were only found on ssp. hololeucus and ssp. graveolens, respectively, in 1977 (McArthur and others 1979b), 1980 (fig. 2), and 1984 (table 1).

In mixed stands where a certain gall form is absent, galls of the type present may occur on the nontypical host as in the following three examples: (1) near Big Rock Candy Mountain, UT, in 1984, 50 ssp. hololeucus bore only callus galls (1-50/plant) whereas 40 ssp. consimilis plants bore no galls and 10 had callus galls (1-6/plant); (2) at Moccasin, AZ in 1984 ssp. turbinatus (10.42/branch) and ssp. hololeucus (2.66/branch) both bore cotton galls to the exclusion of callus galls (table 1); (3) in 1977 along U.S. 89 north from Kanab to Long Valley Junction, UT, the white-stemmed ssp. hololeucus and the green-stemmed ssp. turbinatus, graveolens, and consimilis all bore cotton galls only.

Third, morphologies of cotton and callus galls are controlled by the flies, not the plant. Data from the cline site (table 2) are particularly instructive. Here, cotton formers rarely induce galls on the "wrong" plants (ssp. hololeucus). Dodson (personal communication) also observed a low frequency of cotton galls among the numerous callus galls on white-stemmed C. nauseosus in mixed stands of rabbitbrush in New Mexico. Plants with intermediate morphology are few in number, but they often bear both kinds of galls. Rabbitbrush has a generally inbreeding breeding system (Anderson 1980; McArthur 1984).

Fourth, galls can be used, with restrictions, as taxonomic indicators as we suggested earlier (McArthur and others 1979b). Both gall forms need to be present in the same general area. In that case, the gall forms can be used to help differentiate among subspecies groups. If the callus gall is present the specimen is ssp. albicaulis or hololeucus; the cotton gall indicates ssp. turbinatus, graveolens, or consimilis. The cotton gall may also be on albicaulis and hololeucus, but at a much lower frequency than the callus gall. While the two groups (consimilis, graveolens, and turbinatus versus albicaulis and hololeucus) generally have different stem colors, the colors are not always distinct. The galls have the advantage of being present in winter when leaf and flower characteristics are not present for identification purposes (Anderson 1973; McArthur and others 1979a).

Mace and flower galls are not good subspecies indicators (tables 1, 2). Both occur sporadically among the subspecies examined and neither is as common as cotton and callus galls. The mace gall also occurs on C. viscidiflorus (table 1). It may be induced by a widely distributed, if not common, vector. It is found at higher elevations than the other galls, often on the mountain taxon, C. nauseosus ssp. salicifolius, that has not been observed to bear either callus or cotton galls (McArthur and others 1979b).

nge in Gall Frequency

ls may have different frequencies in space, as the case of ssp. hololeucus at Gould Wash (8.92 ls/branch) versus ssp. hololeucus at Goshen Dam 34 galls/branch), P <0.05 (data from table 1; also McArthur and others 1979b). Galls also e different frequencies over time. For mple, the number of galls in north-central Utah 1984 was down dramatically from previous years. stand we sampled in 1977 at Fountain Green n bore 1.0 callus galls/branch on ssp. oleucus and 0.7 cotton galls/branch on ssp. similis (McArthur and others 1979b). At the e site in 1984, I found no callus galls on 300 . hololeucus plants and only five cotton galls 50 ssp. consimilis plants. I suspect the ent wet weather and cold winters (Richardson others 1982) decimated the fly vector ulations in some local areas.

Gall Inducers

ls on Chrysothamnus are abnormal tissue liferations caused by fly vectors. The cotton callus galls are caused by Aciurina spp. ptera: Tephritidae) (Wangberg 1981). Adult es lay eggs in midsummer. Larvae appear by ust with coincident formation of galls. The ls then serve as the winter home for the larvae ch pupate and emerge the next summer. Cotton callus galls contain one larva per gall.

flower gall, on the other hand, contains eral larvae per gall. The gall I observed is itical to the one illustrated in a photograph arew and Capizzi (1983, p. 75). These authors e that this gall is caused by gall midges tera: Cecidomyiidae). However, Wangberg 0) describes a similar gall and one I have observed--it lacks the cottony center part of flower head, but includes more bracts. This is induced by Procecidochares spp. (Diptera: ritidae), undescribed but called ecidochares spp. B by Wangberg (1980).

mace gall is illustrated by a line drawing rthur and others 1979b) and in a photograph by w and Capizzi (1983, p. 74) who, again, state the gall is induced by gall midges. Dodson sonal communication) confirmed that gall es do indeed induce the mace gall. My ination of galls indicates that the gall ains two larval chambers. Our attempts to flies from this gall have yielded equivocal lts. One Aciurina fly and several small like insects that may have been secondary pants of the gall (Mani 1964) are all that our rts have netted.

data, together with Wangberg's (1980, 1981), that there are considerable gall forms and l-former specificity in Chrysothamnus eosus. Wangberg (1980) gave Aciurina maculata . trixa as the formers for the cotton and s galls, respectively. However, recent work dson (unpublished) indicates that A. loviae may be a causative agent for the cotton . Steyskal (1984) recently revised Aciurina, but it may remain for Dodson's work to unravel the taxonomic difficulty in Aciurina. Aciurina maculata and A. bigeloviae are very similar (Foote and Blanc 1963; and especially Dodson, personal communication). These two species are similar in behavior and morphology (Foote and Blanc 1963; Wangberg 1981). Local sympatric populations of these two species apparently divide the Chrysothamnus nauseosus resource by partitioning green-stemmed (A. maculata) and white-stemmed (A. trixa) rubber rabbitbrushes as minimally overlapping habitats. These fly species choices may also be a clue to the phylogeny of C. nauseosus subspecies.

Similarity of stem tomentum in the two C. nauseosus subspecies groups and the specificity of the two fly species argue for two ancestral lines in C. nauseosus--the green- and white-stemmed groups. In other areas of the two Aciurina species' distribution, they compete for a common resource. I believe that they are in active phases of speciation. Perhaps, the two species are really more than two; sibling species may have developed. Wangberg (1981) gives some evidence for this possibility when he suggests that A. trixa forms four distinct gall types--the common callus and three rarer, sometimes geographically distinct, forms. I have observed that the cotton galls of A. maculata come in apparent different sizes--much larger ones for C. nauseosus ssp. graveolens and ssp. turbinatus than for ssp. consimilis. Might not speciation be going on in A. maculata--the cotton gall former? Determination of differences by fly morphology is extremely difficult. However, Wangberg (1980, 1981) has shown that behavioral differences can be useful. Dodson (personal communication) has recently provided evidence for life history and behavioral differences in sympatric Aciurina gall formers (A. bigeloviae and A. trixa), and demonstrated that isozyme patterns are correlated with morphological and gall-forming traits. Such work needs additional emphasis to solve a set of interesting problems. Aciurina speciation may well gain its impetus, as does the apple maggot fly, Rhagoletis pomonella, another tephritid, by changes in host recognition and in mutation of larval survival genes (Prokopy and Roitberg 1984). Under such a scenario, host specificity changes and consequent sympatric sibling speciation are easily envisioned.

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PHYTOPHAGOUS INSECTS OF GREEN RABBITBRUSH

IN SOUTHEASTERN IDAHO

Michael P. Stafford and James B. Johnson

ABSTRACT: Insects associated with green rabbitbrush were surveyed throughout the summers of 1981-82 in southeastern Idaho. Results indicated that a diverse insect fauna is associated with green rabbitbrush and nearly all plant parts are attacked. The impact of these insects on the host has not been well documented and is in need of further study.

INTRODUCTION

Throughout much of southeastern Idaho, vegetation is dominated by big sagebrush (Artemisia tridentata Nutt.). In many of these sagebrush communities the subdominant shrub is green or low rabbitbrush (Chrysothamnus viscidifloris (Hook.) Nutt.). This species is an important component of these communities. The significant increase in green rabbitbrush after a range fire is important in stabilizing the watershed and restoring site productivity. Species of Chrysothamnus have not received much attention from the scientific community relative to many other plant groups. In particular, the insects associated with rabbitbrush have received little attention from range entomologists. Generally the insects go unnoticed and unstudied until a population outbreak occurs, resulting in considerable defoliation of the host plants.

A diverse insect fauna is associated with green rabbitbrush. This fauna is poorly known both taxonomically and biologically. Therefore, in order to gain a better understanding of the insects and their relationship to green rabbitbrush, we conducted an insect survey in the summers of 1981-82. Our work has been supplemented with information provided by Dr. William. F. Barr, Professor of Entomology Emeritus, University of Idaho.

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METHODS

The majority of our observations and collections came from a 1,500-acre (600-ha) study site located 6 miles (10 km) south of Howe, Butte County, ID, on a portion of the Idaho National Engineering Laboratory. This area is situated on a broad alluvial fan originating at the base of the Lost River Mountains and extending out onto the Upper Snake River Plains. Average elevation is 4,850 feet (1 478 m) and average annual precipitation is 8.7 inches (22 cm). Wyoming big sagebrush (A. tridentata ssp. wyomingensis) is the dominant plant in this area. Green rabbitbrush, however, is interspersed throughout the sagebrush and several large patches of rabbitbrush occur.

We surveyed the insects, using several collecting techniques. Sweeping large amounts of foliage with a standard 15-inch (38-cm) diameter sweep net gave us an indication of the relative abundance of many insect species. The most useful information, however, was provided by close visual observations of the insects on the host. After observing the insects, we either hand-picked them or used an aspirator to remove them from the plant so they could be identified. Plants were also uprooted and examined for root-inhabiting insects. We monitored the seasonal occurrence of these insects by the use of Malaise, windowpane, and pitfall traps.

RESULTS AND DISCUSSION

We have grouped the phytophagous insects into five broad categories: root borers, defoliators, fluid feeders, gall-formers, and flower feeders. Table 1 lists the insect species found to utilize green rabbitbrush as a host. A large number of bees, wasps, and moths visit the nectaries of rabbitbrush; however, we have not included these three groups in this paper.

Root Borers

Two species of beetle larvae bore the root system of green rabbitbrush. The buprestid, Agrilus pubifrons Fisher, is a common inhabitant and causes slight structural damage

to the root structure. Nearly one-half of the plants we examined were previously bored by this species. The boring activity of *A. pubifrons* seems to have little impact on the host.

Less frequently found, at least in the Howe area, are the larvae of the cerambycid, *Crossidius hirtipes allgewahri* LeConte. The impact of this species on the host plant varies, evidently depending upon moisture conditions. Although we never observed any plant mortality caused by *Crossidius*, Barr (1984) observed locally heavy mortality in an area suffering from drought.

Defoliators

A number of insects consume the foliage of green rabbitbrush. All but one species are Coleoptera or Lepidoptera. We observed four species of leaf beetles (Chrysomelidae) feeding on green rabbitbrush. The leaf beetles *Pachybrachys caelatus* LeConte and *Cryptocephalus spurcus* LeConte were found feeding on the leaves in late July and August.

Due to their small size and relative scarcity, their feeding seems to have little impact on the host. The five-striped fleabeetle, *Disonycha latifrons* Schaeffer, is sometimes abundant on rabbitbrush. Larvae were found on the host throughout the summer and adults appeared in late July and August. Although we never observed any noticeable damage to infested plants, Furniss and Barr (1975) reported considerable defoliation in isolated stands. Rarely, we found adult *Trirhabda nitidicollis* LeConte on green rabbitbrush. These plants, however, were in close proximity to a heavily infested stand of rubber

Table 1.--Phytophagous insects utilizing green rabbitbrush in southeastern Idaho

- ROOT BORERS
- Coleoptera
  - Buprestidae
    - *Agrilus pubifrons*
  - Cerambycidae
    - *Crossidius hirtipes allgewahri*

- DEFOLIATORS
- Coleoptera
  - Chrysomelidae
    - *Pachybrachys caelatus*
    - *Cryptocephalus spurcus*
    - *Disonycha latifrons*
    - *Trirhabda nitidicollis*
  - Curculionidae
    - *Anthonomus* spp.
    - 2 undetermined species
- Lepidoptera
  - Noctuidae
    - 2 undetermined species
  - Geometridae
    - undetermined species
  - Coleophoridae
    - *Coleophora* sp.
  - Tortricidae
    - *Synnoma lynosyrana*
- Orthoptera
  - Acrididae
    - *Hesperotettix viridis*

- GALL-FORMERS[1]
- Diptera
  - Tephritidae
    - *Aciurina ferruginea*
    - *Aciurina lutea*
    - *Aciurina* spp.
    - 2 undescribed species
    - *Procecidochares* sp.
    - undescribed species

- FLOWER FEEDERS
- Coleoptera
  - Phalacridae
    - *Olibrus rufipes*
  - Meloidae
    - *Lytta vulnerata cooperi*
    - *Gnathium eremicola*
  - Buprestidae
    - *Agrilus pubifrons*
  - Cerambycidae
    - *Crossidius hirtipes allgewahri*
- Thysanoptera
  - Thripidae
    - *Frankliniella occidentalis*

- FLUID FEEDERS
- Hemiptera
  - Miridae
    - *Lygus desertinus*
    - 4 undetermined species
  - Lygaeidae
    - *Nysius niger*
  - Rhopalidae
    - *Harmostes reflexulus*
- Homoptera
  - Cicadellidae
    - *Aceratagalia poudris*
    - *Ballana hebea* ?
    - undetermined species
  - Cercopidae
    - *Clastroptera* sp.
  - Aphididae[2]
    - *Aphis gregalis*
    - *Aphis ornata*
    - *Brachycaudus helichrysi*
    - *Uroleucon escalanti*
    - *Durocapillata utahensis*
    - *Myzus persicae*
    - *Pleotrichophorus pycnorhysus*
    - *Pleotrichophorus utensis*

[1] From Wangberg (1976).
[2] From Gittins and others (1976).

rabbitbrush (C. nauseosus (Pall.) Britt.). Although Hogue (1970) listed green rabbitbrush as a host for T. nitidicollis, we never observed the larvae on green rabbitbrush, even on rabbitbrush growing adjacent to C. nauseosus infested with Trirhabda. We frequently collected from the foliage two small species of weevils (Curculionidae), both of which are in the genus Anthonomus. Little damage to the plant occurs as a result of their feeding.

Lepidoptera larvae from four families (Noctuidae, Geometridae, Coleophoridae, Tortricidae) utilize green rabbitbrush as a food source. Of these, only the tortricid, Synnoma lynosyrana Walsingham, causes significant defoliation. The developing larvae web leaves and branches together and feed within this webbed mass. Infested plants appear unsightly and less vigorous. Hawkes (1962) reported a reduction in flowering as well.

Although grasshoppers (Acrididae) may occasionally consume rabbitbrush, most species do not utilize it. The species Hesperotettix viridis (Thomas); however, feeds readily on Chrysothamnus and Brusven (1972) reported that in Idaho it is the preferred host.

Fluid Feeders

All above-ground parts of the plant are attacked by fluid-feeding insects in the orders Hemiptera and Homoptera. This group is important because they have the potential to transmit plant diseases. As far as we know, however, no one has investigated insect-transmitted diseases of Chrysothamnus.

Leaf bugs (Miridae) comprise the largest group of Hemiptera feeding on green rabbitbrush. One frequently found species, Lygus desertinus Knight, can be an economically important pest to seed crops in southern Idaho. The false chinch bug, Nysius niger Baker (Lygaeidae), can also be abundant on rabbitbrush. It can be of economic importance on potatoes, but control treatments are rarely needed.

Green rabbitbrush is attractive to several aphid species (Aphididae). Gittins and others (1976) listed eight species that utilize this plant. The impact of these insects on the host depends upon the severity of the infestion. We observed a profuse, flowerlike growth on one plant that was caused by aphids.

A large complex of leafhoppers (Cicadellidae) and one species of spittlebug (Cercopidae) feed on the plant juices also. Early in the summer, leafhoppers are the most abundant group of insects on the plant.

Gall-Formers

Insect-induced galls are frequently found and conspicuous on the plants. Wangberg (1976, 1980, 1981) found that five species of tephritids induced galls on green rabbitbrush in Idaho. In most situations these galls have little apparent impact on the host plant; however, heavily infested plants appear unthrifty and Wangberg (1976) did report some plant mortality.

Flower Feeders

Rabbitbrush flowers are especially attractive to insects. To our knowledge, the impact of this group's feeding activities on seed production and viability has not been documented. Five species of beetles from four families (Phalacridae, Meloidae, Buprestidae, Cerambycidae) consume either pollen or nectar. The meloid beetle, Gnathium eremicola Macswain, has beelike mouthparts and feeds primarily upon nectar. The other species are pollen feeders.

Another flower inhabitant, the western flower thrips (Frankliniella occidentalis (Pergande)) feeds on developing seeds. Furniss (1983) reported this insect destroyed approximately 6 percent of the buds on antelope bitterbrush (Purshia tridentata (Pursh) DC.). The impact of this thrips on rabbitbrush seed has not been quantified.

CONCLUSIONS

Green rabbitbrush is fed upon by a variety of insects, each attacking a specific part of the host plant. Little biological information is known about most of these insects and the impact of their feeding activities is not well documented. Despite the pressure these phytophagous insects exert on their host, we have observed little plant mortality. Therefore, it seems green rabbitbrush, under most conditions, can withstand a substantial amount of insect damage. More research is needed if we are to gain a better understanding of the insect-plant relationships that exist and the role insects have in the regulation of Chrysothamnus populations.

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SNOW DEPTH AND INCIDENCE OF A SNOWMOLD DISEASE ON MOUNTAIN BIG SAGEBRUSH

David L. Sturges and David L. Nelson

\BSTRACT: A snowmold disease of mountain big ;agebrush (Artemisia tridentata ssp. vaseyana), induced by an unidentified fungus, was discovered .n Wyoming in 1973. Snowmold was present on 2)ercent of sagebrush plants where maximum snow iccumulation was less than 16 inches (40 cm), and)3 percent of plants where maximum accumulation :xceeded 47 inches (119 cm). The disease reduces .he canopy area or kills mountain big sagebrush)lants in areas of deeper snow accumulation.

NTRODUCTION

ig sagebrush (Artemisia tridentata) is a hardy hrub, well adapted to the semiarid environment hat typifies much of the West. It has few atural enemies, but mortality attributable to iological agents has been reported. Gates 1964) described an infestation of aroga moth Aroga websteri) on sagebrush-grass rangeland in astern Oregon that affected thousands of acres. wo species of leaf-feeding beetles belonging to he genus Trirhabda also damage sagebrush. ringle (1960) found big sagebrush in British olumbia was defoliated by T. pilosa and felt hat the insect could destroy about 50 percent f a stand. An estimated 2,000 acres (810 ha) f threetip sagebrush (A. tripartita) in Wyoming ere host to T. attenuata (Fisser and Lavigne)61). Voles (Microtus spp.), by girdling the runk of sagebrush, have caused extensive stand image on a localized basis (Mueggler 1967; ibler 1968; Frischknecht and Baker 1972).

1 1973 we discovered a snowmold fungus on mounain big sagebrush (A. t. ssp. vaseyana) in)uthcentral Wyoming. We have since collected ie same fungus on mountain big sagebrush in .ah, Colorado, and other areas of Wyoming. The sease was not found on Wyoming big sagebrush . t. ssp. wyomingensis) or black sagebrush . nova), which grow on sites with little snow cumulation. Our observations suggested that incidence of snowmold on mountain big sagebrush increased as snow depth increased. This study, conducted at the Stratton Sagebrush Hydrology Study Area, was designed to test the hypothesis that occurrence of snowmold is related to snow depth.

per presented at the Symposium: Biology of temisia and Chrysothamnus, Provo, UT, July 13, 1984.

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DESCRIPTION OF THE SNOWMOLD FUNGUS

The snowmold fungus is most prominent immediately after snowmelt when a dense, cottony mycelial growth covers infected sagebrush shoots (fig. 1). Mycelial development occurs while sagebrush plants are covered by snow. The snowmold fungus initially kills a small patch of tissue which then expands in subsequent years as additional healthy tissue is infected. Dead portions within the sagebrush crown are fringed by mycelial mats of recent origin. An entire branch or plant can eventually be killed. The fungus was inactive during the 1977-78 and 1980-81 winters when precipitation was extremely low; however, the organism remained viable and resumed growth when snow conditions were again favorable. Because of the slow advance of the fungus and its perennial character, the incidence of snowmold in any year reflects growing conditions over a number of previous winters.

We have isolated the fungus in other studies and demonstrated its pathogenicity to sagebrush (Nelson and Sturges 1982). It has not sporulated in the laboratory when grown in vitro, nor have we found a sporulating stage in nature. Hyphal septation is typical of the Ascomycetes (Nelson and others 1983), but until a sexual spore stage is found the organism must be placed in the Fungi Imperfecti, meaning sexual reproduction is unknown. Unique knobby projections on the walls of hyphae permit positive recognition of the fungus when hyphae are viewed under the microscope.

STUDY SITE AND EXPERIMENTAL METHODS

The Stratton Sagebrush Hydrology Study Area is located in southcentral Wyoming 18.6 miles (30 km) west of Saratoga. Elevation ranges from 7,600 feet (2 316 m) to 8,100 feet (2 469 m). Meteorological and hydrological information have been collected at the site since 1967. Average annual precipitation was 20.69 inches (52.6 cm), and average annual temperature was 36.8 °F (2.7 °C), during the 14-year period from 1969 to 1982. Approximately 75 percent of precipitation was snow. Strong winter winds relocate snow;

Figure 1.--A dense, web-like mycelium covers the infected portion of a sagebrush plant at the close of snowmelt (left). Closeup view of fungus mycelium on a sagebrush twig (right).

maximum accumulation varies from a few inches on windward slope and ridge areas, to more than 20 feet (6.1 m) in topographically induced depositional zones. Mountain big sagebrush inhabits areas of deeper snow, while Wyoming big sagebrush and black sagebrush are found on sites that retain little snow. Mountain big sagebrush is typically found on soils belonging to the Haggerty series where A and B horizons have a combined depth of 46 inches (117 cm). Mixed stands of Wyoming big sagebrush and black sagebrush grow on soils of the Kimmons series where A and B horizons have a combined depth of 20 inches (50 cm), or on the Roxyal series where the A horizon is 6 inches (15 cm) deep and a B horizon is lacking. Soils belong to the Cryoborall Great Soil subgroup.

The relationship between snow depth and incidence of snowmold was estimated from data collected on five transects in Loco Creek watershed (fig. 2). Transects were established in October 1979 and ranged from 527 feet (161 m) to 1,433 feet (437 m) in length. Loco Creek flows east, and the watershed has predominantly north-facing and south-facing slopes. Transects 1-4 began near the stream channel and extended toward the southern watershed boundary. Transect 5 was in the upper reaches of the watershed and extended in a northeast-southwest direction across a side drainage. All transects crossed a zone of deep snow accumulation and terminated in stands of low-growing Wyoming big sagebrush and black sagebrush. Snow depths were measured from the 1979-80 winter through the 1982-83 winter, by probing with an aluminum rod

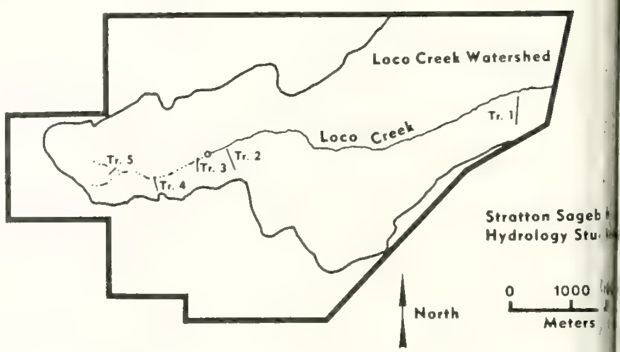

Figure 2.--The relationship of snow depth to incidence of snowmold was determined from data collected on five transects within Loco Creek watershed.

(Jairell 1975) at intervals of 25 feet (7.6 Information was collected about April 1, pri to the start of snowmelt. Accumulation of s on seven index transects that cross major depositional zones in Loco Creek watershed w also measured annually beginning with the 1967-68 winter (table 1). Information from these transects indicated relative size of t snowpack during this study.

The incidence of snowmold was measured in J 1980. Sample sites were located in six str based on snow depths measured earlier in th spring. Strata were: <24 inches, 24-35 inc

able 1.--Annual water content of snow on index transects that cross major depositional zones within Loco Creek watershed

inter	Index transect 1	2	3	4	5	6	7	Yearly average In.	Yearly average Cm	Winter ranking
	Inches							In.	Cm	
967-68	42.9	46.6	55.1	28.2	31.1	77.2	29.0	44.3	113	[1]7
968-69	28.4	31.7	36.9	19.5	20.6	56.2	21.7	30.7	78	12
969-70	25.9	31.6	42.8	28.4	25.2	66.2	23.0	34.7	88	11
970-71	44.4	44.6	55.5	28.1	31.0	71.5	30.0	43.6	111	8
971-72	49.7	44.2	58.5	34.0	32.5	74.4	24.4	45.4	115	6
972-73	31.8	39.0	40.4	24.4	28.2	60.8	25.9	35.8	91	10
973-74	54.1	55.7	70.9	25.4	31.8	82.3	30.0	50.0	127	2
974-75	41.3	52.2	56.8	27.3	32.3	82.0	28.4	45.8	116	5
975-76	50.1	51.8	58.1	30.6	31.3	79.2	27.7	47.0	119	4
976-77	1.5	5.4	8.1	9.8	5.7	15.1	5.4	7.3	19	15
977-78	26.7	30.6	33.6	19.3	19.7	61.7	18.2	30.0	76	13
78-79	67.0	67.5	82.4	42.1	45.4	91.1	42.9	62.6	159	1
79-80	48.8	52.0	53.7	34.1	33.1	81.3	29.6	47.5	121	3
80-81	.0	.5	.3	.1	.2	1.5	.1	.4	1	16
81-82	45.2	42.2	52.1	31.4	28.7	74.5	26.7	43.0	109	9
82-83	21.9	28.1	32.3	18.8	22.1	51.9	20.3	27.9	71	14

he winter with the greatest snow accumulation in the 16-year period is ranked #1, the winter with least now accumulation is ranked #16.

-47 inches, 48-59 inches, 60-71 inches and >71 iches (<60 cm, 61-90 cm, 91-120 cm, 121-150 cm, 1-180 cm, and >180 cm). The location of iowmold sample sites in each stratum was ran- mly selected from snow measurement points in ie stratum. An attempt was made to place four iowmold sampling sites within each snow-depth ratum. Placement of snowmold sampling sites i each transect is shown in figure 3.

iowmold incidence was measured on belt tran- ects 4.4-feet (1.3-m) wide which extended rpendicularly from snow transects so that igebrush on individual belt transects would ive a uniform snow cover. Orientation of belt transects was randomly determined. The first 25 sagebrush plants on a belt transect were categorized as either infected or not infected, based on the presence of mycelium from the previous winter. The height of the first 10 plants on a belt transect was recorded. The distance to the 25th plant was also recorded to enable sagebrush density to be calculated.

STATISTICAL ANALYSIS OF DATA

Data relating snowmold incidence to snow depth were analyzed by analysis of variance within a factorial experimental design. The variance

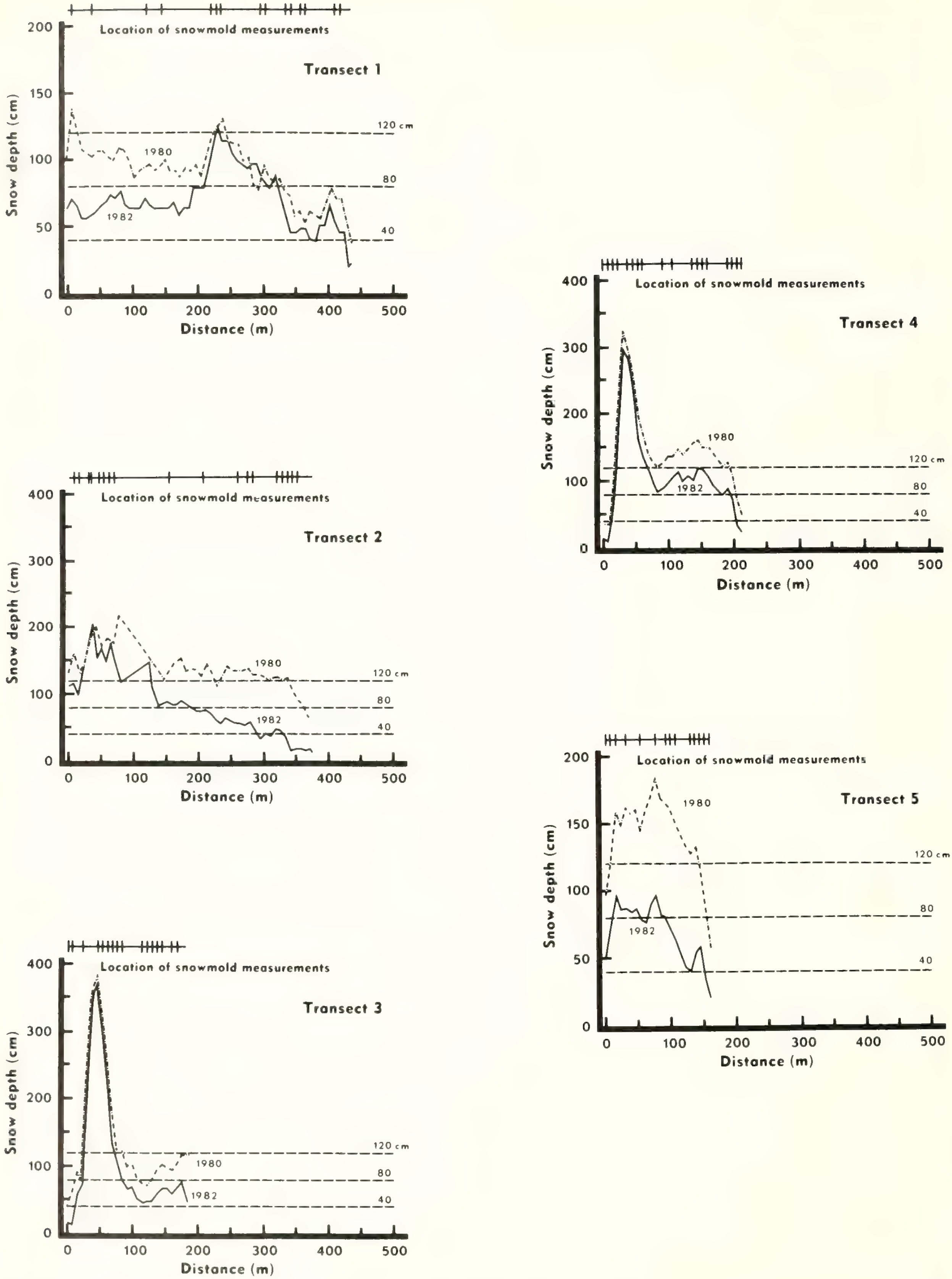

Figure 3.--Snow depths in the 1979-80 and 1981-82 winters on the five transects where incidence of snowmold was measured. The location of snowmold sampling points is also shown.

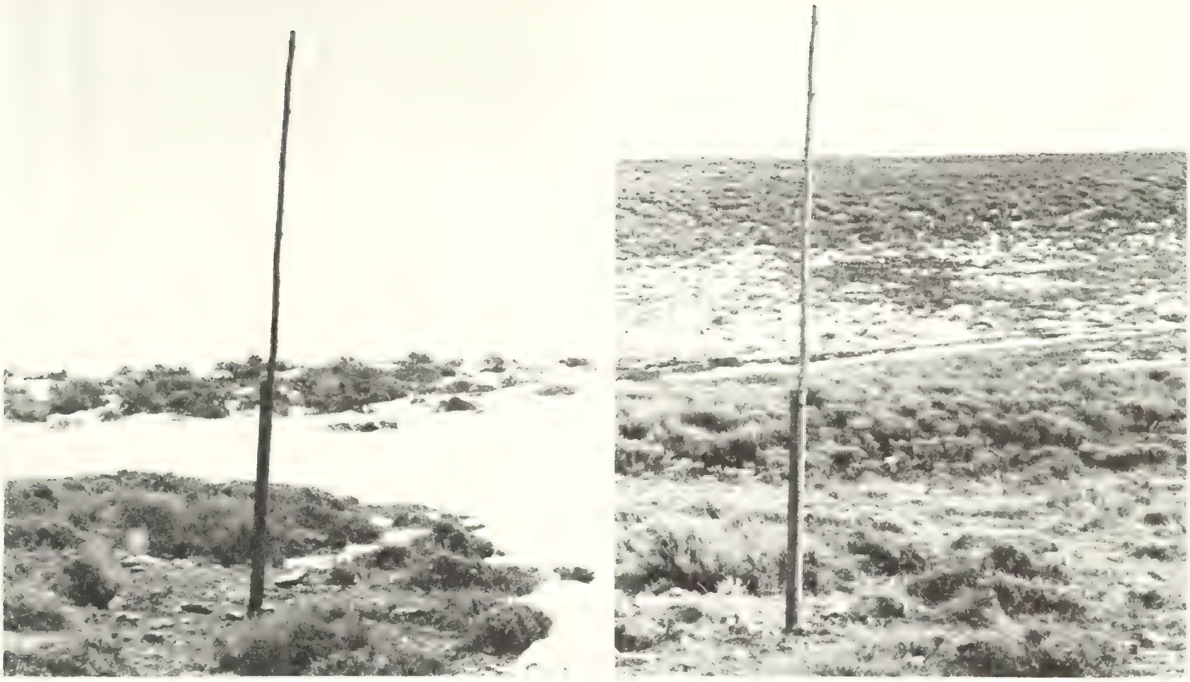

Figure 4.--More than 11.5 feet (350 cm) of snow accumulated on transect 3 in the incised channel of Loco Creek at maximum accumulation in the 1979-80 and 1981-82 winters (left). The fungus was inactive in winters when snow failed to cover sagebrush, indicated by conditions on transect 3, April 4, 1981 (right).

model permitted identification of significant differences in snowmold incidence between transects, between snow depth strata, and an interaction between depth strata and transects. Differences in snowmold incidence between snow depth strata were tested for significance using procedures described by Gabriel (1963) for dichotomous data. Sagebrush density data and sagebrush height data were also subjected to analysis of variance. Treatment means were tested for significance using Kramer's modification of the Tukey multiple range test (Dunnett 1980). A 0.05 probability level indicates statistical significance in this paper.

RESULTS

Snow Accumulation

Strong southwesterly winds relocate snow following precipitation events. The depth of snow accumulation at any location reflects the interaction between winter precipitation, vegetation height, and topographic position. Annual variations in snow accumulation between 1968 and 1983 are shown in table 1 for index transects in Loco Creek watershed. The pattern of deposition on the five transects utilized for snow measurements in this study was consistent from year to year, though annual snow depths were quite different. Yearly variations are indicated by data for the 1979-80 and 1981-82 winters (fig. 3). The deepest snow, more than 10 feet (305 cm), was present on transects 3 and 4 which cross the incised channel of Loco Creek.

Based on 16 years of information from permanent watershed transects, snow accumulation in the 1979-80 winter was the third highest, accumulation in the 1981-82 winter was average, and accumulation in the 1982-83 winter was the third lowest (table 1). Precipitation in the 1980-81 winter was the lowest ever recorded and snow failed to cover sagebrush plants (fig. 4).

Relationship of Snow Depth to Snowmold Incidence

The snowmold disease acts in a chronic rather than acute fashion. Presence of the fungus in a sagebrush stand reflects snow conditions over a number of preceding winters. Data on snowmold incidence were collected after snowmelt in 1980, but snow accumulation in the 1979-80 winter was very large. We felt that the relationship between snow depth and snowmold incidence should be based on snow conditions in an average winter, rather than conditions in a winter with either an extremely large or an extremely small snowpack. Thus, data collected in the 1981-82 winter, which represented an average snowpack, were used to relate incidence of snowmold to snow depth. A number of snow-depth strata on different transects lacked a single observation when snow depths measured in the 1981-82 winter were related to

snowmold incidence. Consequently, snow depths were restratified into four strata: 0-15 inches, 16-31 inches, 32-47 inches, and >47 inches (0-39 cm, 40-79 cm, 80-119 cm, and >119 cm).

Average incidence of snowmold for the four snow-depth strata is shown in figure 5. Differences attributable to transects and to snow-depth strata were significant. The interaction between snow-depth strata and transect location was not significant, indicating that the increase in snowmold incidence with increasing snow depth was similar on all transects. Incidence was very low where snow was less than 16 inches (41 cm) deep, but increased sharply as snow depth increased to 47 inches (119 cm). Differences in snowmold incidence between the two deepest snow-depth strata were not significant.

Relationship of Snow Depth to Sagebrush Density and to Sagebrush Height

The height and density of sagebrush were also related to snow depth. Average stand density decreased 34 percent going from a 0 to 15-inch (0 to 39-cm) snow depth, to a 16 to 31-inch (40- to 79-cm) depth, while average stand height nearly tripled (fig. 5). These figures reflect replacement of Wyoming big sagebrush and black sagebrush, which grew in locations where snow was less than 16 inches (40 cm) deep, by mountain big sagebrush, which grew in locations where snow was more than 15 inches (39 cm) deep.

Differences between sagebrush density in the three deepest snow-depth strata were not significant. The interaction between snow depth and transect location was significant for sagebrush density, unlike the analyses for incidence of snowmold or sagebrush height. The change to mountain big sagebrush from black sagebrush-Wyoming big sagebrush is not always sharply defined, particularly if there is a gradual change in snow depth with increasing slope elevation. Thus, sample sites on some transects where snow was defined as less than 16 inches (40 cm) deep were inhabited by mountain big sagebrush, while other sample sites defined as having snow deeper than 15 inches (39 cm) were inhabited by black and Wyoming big sagebrush.

DISCUSSION

Study data indicated that about 16 inches (40 cm) of snow were required for growth of the snowmold fungus. It is unlikely that snow depth per se was the primary factor influencing development of the disease. Rather, areas of deeper snow probably provide a suitable environment for growth. Laboratory studies show that snowmold fungus is adapted to a low-temperature regime (Nelson and Sturges 1982). Optimum in vitro growth of fungus mycelium occurred near 53.6 °F (12 °C), but some growth did occur at a temperature of 24.8 °F (-4 °C). The threshold snow depth that enables the fungus to grow probably varies somewhat with climatic regime. The crucial factor is having a snowpack temperature

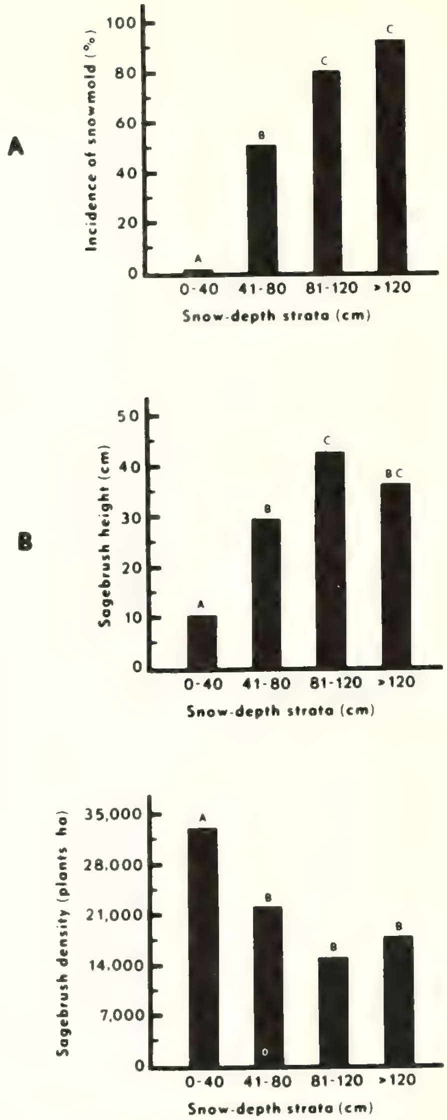

Figure 5.--The relationship between snow dept and (A) incidence of snowmold, (B) sagebrush height, and (C) sagebrush density. Any two means having different letters are significar different.

at or slightly below the freezing point of w sufficiently long for the fungus to grow.

Excessively cold temperatures in the snowpac probably prevent appreciable fungus growth i early winter months at the Stratton site. Maximum daily air temperatures are below fre by mid-November and remain below freezing un late March. In the spring, the snowpack mus warm to 32 °F (0 °C) before melt begins. On snow melts, sagebrush is exposed to the desi cating effects of the atmosphere. Thus, the a relatively short period of time in the spr when snowpack temperatures are warm enough f appreciable growth of the snowmold fungus.

Development of the fungus probably takes pl while the snow surface is well above the

ebrush canopy. Snowmelt is extremely rapid e the snow surface reaches the sagebrush opy. Vegetation reradiates incoming short-e solar radiation as long-wave radiation, ch greatly accelerates snowmelt. Melt rates 2.4 inches (6 cm) of water per day have been sured at the Stratton site (Sturges 1977). uming snow has a 35 percent water content, ut 6.7 inches (17 cm) of snow are required to vide 2.4 inches (6 cm) of water. Thus, it is sible for snow to completely melt from a nd of Wyoming big sagebrush and black sage-sh in a single day.

depths under 16 inches (40 cm) coincided a low incidence of snowmold, and also with s inhabited by stands of Wyoming big brush and black sagebrush. The low inci-e of snowmold in these stands might be ibuted to a resistance of black sagebrush Wyoming big sagebrush to snowmold. Tests we ucted in the laboratory demonstrate that the us can grow on both the Wyoming and basin t. spp. tridentata) subspecies of big brush as well as black sagebrush. Thus, we eve that the low incidence of snowmold on e sites reflects the fact that about 16 es (40 cm) of snow are required to provide icient time for the fungus to fulfill growth irements, rather than reflecting differences usceptibility of sagebrush subspecies to mold.

mold caused a substantial reduction in moun-big sagebrush cover at the Stratton study tion. Transect 2 traversed an area where effects of spraying sagebrush on soil water and on vegetation production have been ied since 1969 (Sturges 1983). Snowmold was observed at the site in 1973. The canopy r of mountain big sagebrush was measured in before the fungus was active and again in after it had been active for a number of s. Canopy cover decreased 34 percent in 12 years, a significant reduction attribu-primarily to the snowmold.

ative production measurements, which included current annual growth of sagebrush, also ated a decline in importance of sagebrush. l vegetative productivity decreased from an ge of 1,271 lb/acre (1 424 kg/ha) in the r period, 1971-73, to an average of 916 re (1 026 kg/ha) in the 2-year period, -81. Annual forb and grass production dif-by only 6 lb/acre (7 kg/ha) in the two ds. Thus, the decrease in total production tributable to loss of sagebrush.

ional studies are needed to determine the gical role of the snowmold fungus in the ain big sagebrush zone. Lack of suitable s has prevented the use of biological control ds in management of sagebrush rangeland. may be a potential for using the snowmold ism to thin mountain big sagebrush stands environmental conditions are suitable for rowth.

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Section 6. Ecology

SAGEBRUSH OVER TIME:

A PHOTOGRAPHIC STUDY OF RANGELAND CHANGE

Kendall L. Johnson

BSTRACT: The nature of the big sagebrush zone in resettlement times is an enduring question that annot be answered definitively. Comparison of resettlement photographs with modern retakes of he same sites, however, provides useful informa-ion. This study compares 20 current photographs f Rocky Mountain sagebrush rangeland with those aken by William H. Jackson during the 1870's as a ember of the U.S. Geological and Geographical urvey of the Territories (Hayden Expedition). The hotographs were selected to illustrate different ite responses: (1) sagebrush decrease or destruc-ion, (2) sagebrush stability, (3) sagebrush ncrease or establishment, and (4) combination ffects. Comparative analysis indicates that: (1) he reaction of big sagebrush stands to use and anagement is highly site-specific and a function f the kind of use and site characteristics; (2) hifts in composition and density of species have ccurred but their magnitude cannot be assessed, lthough they probably range from slight to major hange; (3) there has been no major shift in sage-rush distribution as a result of use; and (4) the ppearance of the landscape today is a fair indi-ation of its appearance in presettlement times.

NTRODUCTION

erhaps the most enduring question among students f western plant ecology is the nature of the big agebrush zone prior to European settlement. Was t mainly a grassland with sagebrush present only s a savanna? Many people think so, which leads o the belief that much of the present sagebrush-ominated land is the result of early and con-inued abusive use. The thought has become a kind f conventional wisdom, and the source of many sagebrush-infested" statements (Cottam and tewart 1940).

r was the big sagebrush zone largely a shrubland, ith sagebrush as a clear dominant? Many students f sagebrush think this was the case, pointing to he climax adaptation of the shrub. This leads to elief that sagebrush stands may have increased in ensity as a result of land use, but do not repre-ent a major shift in vegetation type. In this iew, the sagebrush zone appeared then much as it oes now, at least in broad-scale or regional erms (Hironaka 1979).

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aper based on an address presented at the ymposium: Biology of Artemisia and hrysothamnus, Provo, UT, July 9-13, 1984.

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It is a controversy that will never be satisfactorily resolved for a very simple reason: lack of information. There are no definitive records of presettlement vegetation, hence proponents of any position in the argument must rely on indirect and circumstantial evidence which, by its nature, is open to different interpretations. The result is often that additional heat, but little light, is directed to the question.

It is true, however, that some kinds of circumstantial evidence are more compelling than others. Among these are landscape photographs taken before the effects of settlement, especially those of cultivation and livestock grazing, became significant. Comparison of such photographs with modern retakes of the same scenes offers a degree of insight into pristine vegetation not otherwise available. This study is an examination of ecological change in central Rocky Mountain sagebrush rangeland, based on comparison of photographs separated by well over 100 years. In this effort I try to show how sagebrush rangeland looked in the 1870's and how it looks today, speculate on the probable causes of the changes observed, and from that infer the relative ecological stability of the sites involved.

This pursuit was made possible by the efforts of William Henry Jackson, an early and exceptionally able practitioner of the then-new art of landscape photography in the 1870's. His photographs make it possible for us to gain some insight into the role of big sagebrush on presettlement rangeland and how that role may extend into the present time.

THE EARLY WEST IN DESCRIPTION

Aside from the remaining relict areas, large and small, the only evidence of early western vegetative conditions lies in the descriptions found in the journals, reports, and diaries of the first explorers and travelers. Their observations, however, were normally fragmentary, frequently conflicting, and sometimes puzzling. This is because nearly all of the early observers were in the West for practical reasons having nothing to do with vegetation, aside from its value as forage for trail stock. Most were simply traveling through the intermountain country to Oregon and California. A few were trappers, prospectors, hunters, and later, homesteaders. Almost none were observers of the country for itself. Therefore, their descriptions of vegetative conditions were usually both incidental and very general. For instance, Wislizenus (1912) observed that west

of Fort Laramie "the country continued hilly, sandy, poor as to grass, but so much the richer in sage brush," a description that leaves the reader wondering about the relative values of "poor" and "richer."

A major consequence is that the historical records are open to various and sometimes sharply different interpretations. For instance, Stewart's (1941) survey of historical records of Utah range ecology emphasized an abundance of grass in presettlement times. On the other hand, Vale (1975) maintained that the historical records established sagebrush as an ecological dominant in the intermountain West. Indeed, Young and others (1979) argued that the historical records could be used to justify any preconceived opinion of pristine vegetation. While that position may be extreme, there is no doubt that written history does not provide a definitive description of presettlement vegetation.

There are two partial exceptions to this general pattern: the scientific and military surveys, both designed to obtain specific information about the western territories. The scientific surveys were prompted by construction of the transcontinental railroad, which generated professional and public curiosity about the West. After the Civil War, Congress authorized several formal efforts to describe the land and its resources (Schmeckebier 1904). Surveys headed by Clarence King (1867-72), F. V. Hayden (1867-79), John Wesley Powell (1871-79), and George M. Wheeler (1871-79) explored, mapped, and documented in great detail major portions of the West, before being discontinued in favor of the U.S. Geological Survey in 1879.

The other main source of early formal information about the West was the U.S. Army. Charged witn defense during the Indian Wars, the Army mounted numerous survey expeditions to the West to meet its strategic and tactical responsibilities. Prominent examples are the two Fremont expeditions across the Rocky Mountains in the 1840's (Fremont 1845), the 1849-50 Stansbury expedition to the Great Salt Lake (Stansbury 1852), the 1874 Custer expedition to the Black Hills (Ludlow 1875), and the 1859 Simpson exploration of the Great Basin (Simpson 1876).

All of the scientific and military surveys gained a wealth of detailed and reliable information on the natural resources of the West. But it must be remembered that the primary objective of survey personnel concerned with vegetation was the occurrence of species rather than the relations between them. Indeed, ecology had yet to be defined as a formal discipline, and so survey descriptions of vegetative conditions, while improved, were still not definitive.

Probably the most significant Survey was the long-running (1867-79) U.S. Geological and Geographical Survey of the Territories, informally known as the Hayden Expedition for its leader and director Dr. Ferdinand Vandiveer Hayden, a medical doctor become geologist. Dr. Hayden was instrumental in persuading Congress to authorize a series of annual expeditions to the central Rocky Mountains, including the famous 1871 Yellowstone survey that proved instrumental in establishment of the first national park. It is notable that the 1871 survey achieved its significance through the then-new medium of landscape photography. Through it verbal descriptions of the natural wonders of the Yellowstone, previously rejected as only tall tales, acquired visual support and thus credibility. So photography was a development that became a standard part of survey organization.

THE EARLY WEST IN PICTURES

A survey staff typically included several professional scientists in disciplines such as geology, minerology, botany, soils, zoology and meteorology. Due to the need for pictorial representation of striking features of the landscape, several of the surveys also employed or allowed volunteer service of artists. The noted landscape painter Thomas Moran, for instance, accompanied the 1871 Hayden expedition to the Yellowstone. Several of his landscape oils of later years were of subject first sketched on the trip, including the now-famous painting of Yellowstone Falls. Once photography became a usable field technique, all of the surveys used it to provide visual evidence of notable features. The early survey photographers, John K. Hillers (Fowler 1972), Timothy H. O'Sullivan (Horan 1966), and William H. Jackson (Jackson 1940), were of great service in attaining survey objectives, and together created a scientific and artistic record of enormous value.

Jackson and the Hayden Expeditions

William Henry Jackson was for 9 years (1870-78) the staff photographer for the several Hayden expeditions. His survey service was the foundati of a distinguished photographic career and the basis of his critical standing as a photographer (Szarkowski 1963). Through the expeditions he became not only one of the first, but one of the best, landscape photographers.

Jackson's association with the Survey began almo accidentally, as the result of a chance encounte with F. V. Hayden on the newly constructed trans continental railroad in 1869. Jackson was takin pictures of the railroad and of natural features near the grade for a commercial purpose. The ne summer, Hayden stopped at Jackson's studio in Omaha on his way to conduct the 1870 Survey in Wyoming Territory, and invited him to accompany the expedition as official photographer. Althou he was not offered a salary, Jackson accepted readily for only keep and expenses, control of th negatives, and the satisfaction of contributing art to science!

This was the first time the Survey had carried a photographer, and Hayden reported that Jackson produced about 400 negatives on the trip (Hayden 1871). By the end of the expedition, Jackson ha become a permanent and salaried member of the Survey staff. Thus began the photographic library

hat caused Current (1978) to observe: "They [the hotographs] remain the earliest benchmark against which change--geological, ecological, botanical--an be measured." It is against this background hat the photographs of natural landscapes taken y W. H. Jackson become significant. They open a window on the past through which comparisons with modern conditions can be made. The photographs help evaluation of the early writings and improve deductions on how, why, and to what extent changes have occurred. Jackson's work is an original contribution to photography, and an example of art n the service of science.

ETHODS

his study is an appraisal of ecological changes n the sagebrush-grass rangeland of southern Wyoming, southern Idaho, and northern Utah. It is based on a comparison of Jackson photographs with modern retakes over 100 years later, employing mainly the photographs taken during the 1870 Hayden expedition, with some additional views from he 1871 and 1872 expeditions, and from an 1869 trip along the railroad. These were collated by Jackson as part of a descriptive catalog (Jackson 875). All views now available in the USDI Geological Survey photographic library in Denver were inspected, and a decision made on their suitability for comparative study. Over 100 photographs were chosen that best illustrated rangeland conditions of the 1870's, and that offered a reasonable prospect of relocation. Twenty photosites that illustrated different responses to the use and management of sagebrush-grass rangeland over the past century were selected for this study fig. 1).

Procedures

Over a 12-year period, 1974-1985, each Jackson photosite was relocated through time-consuming search in the field, aided by knowledge of the countryside and comparison of expedition maps and reports with modern references. Once the general location was found, the exact photopoint was relocated by detailed inspection of photo features. In a few cases, change had either obliterated the photopoint or made it impossible to see the subject from the original point. In such instances, suitable offset views were taken. All photographs were relocated with enough precision for comparison.

Once a photopoint was located, comparison photographs on both black and white and color films were taken, and appropriate notes made of date, time of day, line-of-sight direction, and photographic exposure. Directions to the site were recorded, and the point was marked on the ground for subsequent visits.

Information gathered on the site included a list of major plant species growing in the photopoint area (species nomenclature generally followed Hitchcock and Cronquist [1973] except that the Triticeae grasses were named according to Dewey [1984]). A ground-cover index (GCI) was generated by a 50- or 100-pace transect located on the photo line of sight, adjusted for physical conditions (NAS/NRC 1962). At every step of the right foot (1 pace), records were made of cover conditions (bare ground, rock, litter, vegetation) defined by a point at the toe of the boot sole. The GCI was regarded as the percentage of covered ground (total of all classes except bare ground).

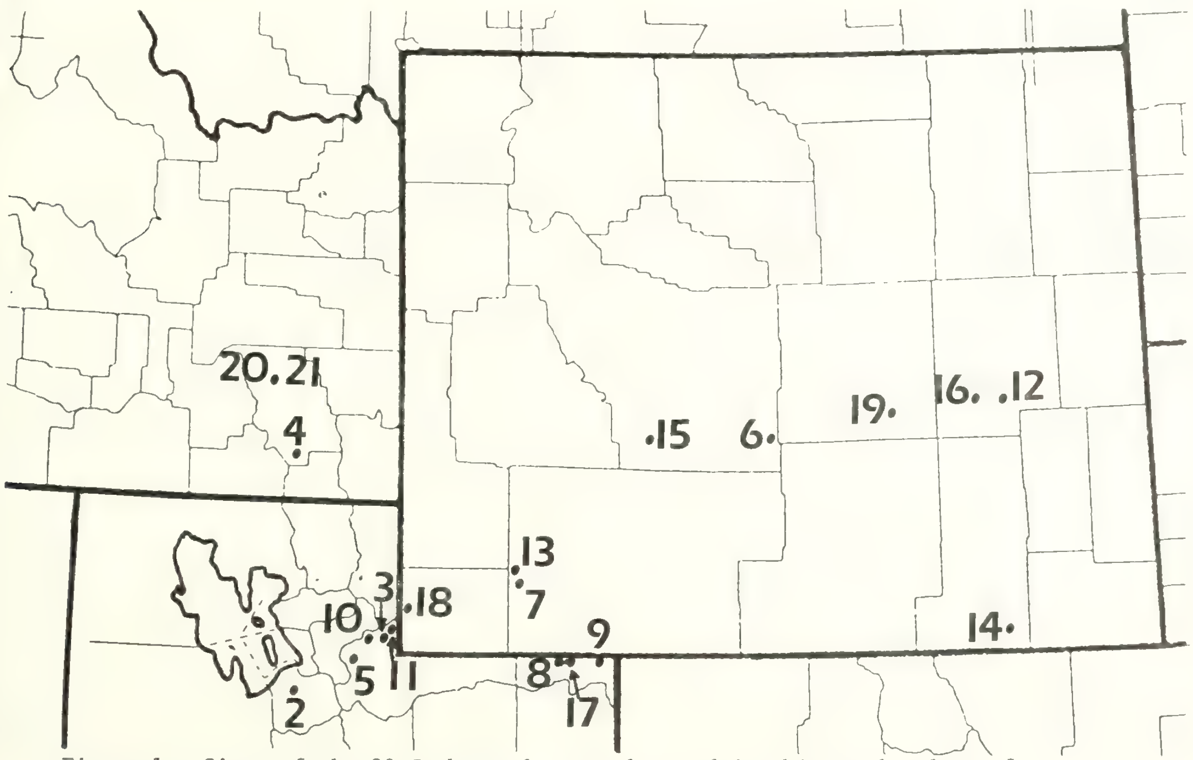

Figure 1.--Sites of the 20 Jackson photographs used in this study, drawn from his 1869 railroad trip and the 1870, 1871, and 1872 Hayden Expeditions. Numbers correspond to figures at the end of this paper.

Descriptive notes were made of site conditions, erosion patterns, soil characteristics, grazing use, and cultural changes. Field estimates of apparent range condition (ARC) and of apparent range trend (AT) were completed.

Subsequently, one or more visits were made to each photosite to obtain comparison photographs having the same light conditions as the original Jackson view. These photographs were made as close to the original date (determined from expedition records) and time of day (determined from photo shadow patterns) as possible. At this time all previously gathered site information was reviewed and additional observations were made.

Analysis

The several Hayden expeditions produced thousands of photographs of the presettlement West. Those surviving to the present provide much valuable information about the land. Identification of range sites, vegetation types, dominant plant species (especially shrubs), and a general appraisal of apparent range condition are all possible in the photographs. The collection is particularly valuable in its illustration of conditions before the advent of cultivation and domestic livestock. We see in the Jackson pictures pristine western rangeland.

But as estimators of early ecological conditions, the photographs have several inherent limitations. First and most important, interpretation is restrained both by the nature of the expedition and by the photographer's choice of subject. The basic perspective of the Survey was geological, and so many photographs are of bluffs, pediments, and unusual rock formations--more than their relative importance in the landscape might merit. In addition, Jackson was interested in the most photo-worthy subjects from an artistic, as well as a naturalistic, point of view. This caused a definite bias in subject selection toward the striking features of the landscape, especially on the often featureless rangeland traversed by the 1870 survey. In a technical sense important to the present purpose, Jackson did not take pictures of rangeland as such. Therefore, evidence of the ecological conditions of the day is usually incidental to the primary focus of the photographs.

Second, and also very important, the shallow oblique angle and distant orientation in the normal perspective of landscape photographs rule out detailed evaluation of many ecologically important characters. Although dominant plant species usually can be recognized, no definitive information can be gained on species composition, relative plant density, or ground cover. Analysis is confined to the perspective of the camera lens.

Another limitation occurred because the bulky cameras, slow films, and laborious wet-plate photographic process of the 1870's were often unequal to the atmospheric conditions of time and place. Few pictures were taken on windy days, for instance, because rapid movement of vegetation exceeded photographic capability. In addition, blowing dust made wet-plate negatives even more difficult to handle properly; under such circumstances photographs were usually not taken, even though potentially valuable studies were missed.

Lastly, the physical conditions of 1870 travel sometimes imposed restrictions. The number of glass plates an expedition could carry was limited, chemicals and water were sometimes in short supply, accidents and mishaps occurred, and backtracking was infrequent. Consequently, glass plate negatives destroyed in accidents often cou not be replaced, and views flawed by errors in exposure or development were frequently retained.

These characteristics limit, but do not destroy, the utility of the photographs as baseline evidence in a study of ecological change. We canno identify or conclude as much as we might wish, b what is possible is also valuable.

Presentation

The comparison of each Jackson photograph with i retake was based on site description, appraisal (physical/cultural and ecological), and historic or pictorial qualities. Based on the overall analysis, each site was assigned to one of four change classes:

1. Sagebrush decrease or destruction
2. Sagebrush stability
3. Sagebrush increase or establishment
4. Combination effects.

The photo pairs are presented sequentially withi the four change classes, without regard to geographic location. The photosites are identified by the place names assigned by Jackson, and all f the original photographs carry the USGS collection numbers. Figure numbers are identica to the photosite numbers in figure 1.

RESULTS

Sagebrush Decrease or Destruction

Most discussion of the ecological history of bi sagebrush (Artemisia tridentata) does not inclu an argument for its decrease. It is well to remember, however, that European occupation of e sagebrush ecosystem has induced numerous instan s of precisely that consequence.

View of the Wasatch Mountains (fig. 2).--One of the most graphic examples of sagebrush decrease has taken place in the Salt Lake Valley. The photosite is now in urban Salt Lake City, and cannot be relocated precisely. But it does not matter, for it is obvious that a large area of g sagebrush has been permanently removed. Estima s of GCI, ARC, and AT are inapplicable at this si due to the advanced stage of urban development.

It is reasonable to suppose that the 1872 photo also represents the presettlement conditions of 5

years earlier, and can be used to help evaluate conflicting verbal descriptions of the Salt Lake Valley such as those of Clayton (cited in Stewart 1941), who reported much grass, and Hayden (1870) who called it "a vast sage plain". It appears that Hayden had the more correct general description while Clayton may have described the somewhat better-watered areas of the initial settlement.

Castle Rocks (fig. 3).--While not as extreme as figure 2, other photographs show evidence of use and management resulting in the decrease of sagebrush. The 1869 photograph of Castle Rocks at the head of Echo Canyon in Utah shows a vigorous, dominant stand of big sagebrush. Based on modern information, we can speculate that the size and density of the shrubs must surely have suppressed herbaceous production. Ecological change evident in the retake photo is certainly due to repeated fires, likely started by locomotive embers on the railroad grade which destroyed the original photopoint. Marks of at least two fires are evident. High on the slope, secondary succession since an early fire has produced a sparse stand of bluebunch wheatgrass (Pseudoroegneria spicata) and Indian ricegrass (Oryzopsis hymenoides), with scattered rubber rabbitbrush (Chrysothamnus nauseosus), serviceberry (Amelanchier alnifolia), Utah juniper (Juniperus osteosperma), and big sagebrush.

A more recent fire lower on the slope, generally below the road cut as indicated by the juniper skeletons, has removed the bluebunch wheatgrass. A fairly even stand of needle-and-thread (Stipa comata), Great Basin wildrye (Leymus cinereus), cheatgrass (Bromus tectorum), and Indian ricegrass dominated by thistles (Cirsium spp.) is now in place. The slope is formed of alluvial deposits, with a great deal of water-worn cobble on the surface. Generally the hillside is unstable (GCI = 61, about half cobble), and in low fair condition with a slight upward trend. If there is a continued absence of fire, big sagebrush may again establish dominance, but more likely it has been permanently reduced on this site.

Camp on Gooseberry Creek (fig. 4).--The influence of agricultural development in southern Idaho can be seen in the photo comparison of a stream bottom surrounded in 1871 by sagebrush-grass uplands. A small relict area, pinched off between a road and the cultivated valley bottom, on the far channel slope indicates that big sagebrush then formed an open savanna (Hull and Hull 1974). The shrub now provides about 20 percent crown cover within a dominant stand of bluebunch wheatgrass and a rich variety of forbs, mostly arrowleaf balsamroot (Balsamorhiza sagittata), yellow salsify (Tragopogon dubius), western yarrow (Achillea millefolium), scarlet gilia (Gilia aggregata), and many others. Accumulation of litter has produced a dense ground cover (GCI = 94), indicating that the site has not been grazed or burned for many years. Range condition is high good to excellent with a slight downward (stagnant) trend.

Outside the relict area native vegetation has been replaced by intensive agriculture. The rolling uplands are in dryland wheat production and the valley bottom grows barley and alfalfa. Like hundreds of thousands of acres elsewhere, former sagebrush lands are now farmland.

Death Rock (fig. 5).--A uniform stand of big sagebrush occurred on the flood terraces at the mouth of Echo Canyon, already in 1869 the site of Echo City, Utah. In the years following, the area became part of a major transportation corridor. The original grade of the old Lincoln Highway was built right through the photopoint. Several railroad and highway grades plus interchanges for both are now in the near vicinity. The construction activity plus one or more fires have destroyed the sagebrush stand. In its place now is a weedy herbaceous community dominated by prickly lettuce (Lactuca serriola), tumblemustard (Sisymbrium altissimum), pepperweed (Lepidium perfoliatum), yellow salsify, and cheatgrass. Fair amounts of Louisiana sagewort (Artemisia ludoviciana) and needle-and-thread can be found. Scattered clones of Gambel oak (Quercus gambelii) and skunkbush (Rhus trilobata) inhabit the rocky outcrops with an occasional big sagebrush. The old highway grade is almost entirely rubber rabbitbrush.

The numerous weeds have produced abundant litter (GCI = 90), but range condition is very low. Long-term trend is slightly upward, but it is by no means certain that secondary succession will reestablish the former sagebrush stand to any significant degree, even though vigorous sagebrush communities persist nearby.

These examples could be multiplied across the entire sagebrush ecosystem. Nearly every acre of upland now devoted to intensive agriculture has been broken out of natural vegetation dominated by sagebrush. Most of the buildings, roads, canals, railroads, and other forms of construction have occupied former sagebrush land. Together with repeated fire, these kinds of changes have reduced the presettlement distribution of sagebrush, often permanently.

Sagebrush Stability

A surprising number of big sagebrush sites photographed by Jackson evince no discernible change more than 11 decades later. Keeping in mind that the photographs do not allow detailed evaluation of changes in plant composition or density, site stability is still evident.

Granite Ridges on the Sweetwater (fig. 6).--A protected cove off the Sweetwater River in central Wyoming supported a vigorous, dominant stand of big sagebrush in 1870. Today big sagebrush remains dominant, joined by rubber rabbitbrush and low rabbitbrush (Chrysothamnus viscidiflorus). The herbaceous population is dominated by needle-and-thread, Indian ricegrass, prairie sandreed (Calamovilfa longifolia), purple prairie clover (Petalostemon purpureum), and prickly pear (Opuntia polyacantha). Low use is indicated by litter buildup in the crowns of plants and in the between-plant spaces (GCI = 67).

Aside from the increase in size and density of the juniper trees in the rocks, this sandy, protected site retains in every way its appearance of 1870. Both the sagebrush dominance and the productive potential of Jackson's time remain, indicating a high degree of site adaptation and ecological stability [ARC: high good; AT: stable].

Badlands on Blacks Fork (fig. 7).--Stability of another kind can be seen in the sharply etched vegetative types surrounding Church Buttes in southwestern Wyoming. The 1870 view shows a stark sandstone outcrop surrounded by a highly saline outwash area from the butte, and areas of deep sand accumulation. Vegetal cover remains very low (GCI = 13) on the saline outwash, composed almost entirely of saltsage (*Atriplex gardneri*) and shadscale (*Atriplex confertifolia*). Big sagebrush and low rabbitbrush remain dominant on the sandy "islands" with an understory (GCI = 70) of Indian ricegrass, needle-and-thread, western wheatgrass (*Pascopyrum smithii*), and annual forbs.

The productive potential of this site was and remains very low. More than a century after the original photograph there is no visible change; the photographs could be interchanged without loss of information at either time [ARC: good; AT: stable].

A Natural Cave (fig. 8).--In 1870 Jackson photographed a sandstone cave near the confluence of Henrys Fork and the Green River which is now just off Linwood Bay on Flaming Gorge Reservoir. The surrounding slopes form a very sandy range site dominated in 1870 by shrubs. The retake view shows a marked increase in size and density of the distant trees but otherwise very little change. The shrubs are primarily big sagebrush with some low rabbitbrush and a few fourwing saltbush (*Atriplex canescens*). Herbaceous species are mainly needle-and-thread, Indian ricegrass, sand dropseed (*Sporobolus cryptandrus*), hoary aster (*Machaeranthera canescens*), fringed sagewort (*Artemisia frigida*), and prickly pear. On this site, shrub density and ground cover (GCI = 62) appear the same as they were in 1870. Were it not for the change in the junipers, the two views would be virtually identical [ARC: high fair to low good; AT: stable].

The photosite is now within Flaming Gorge National Recreation Area, and the reservoir has created greater physical isolation. Both factors will work toward future stability in use and management of the area.

Scene Near the Head of Red Creek (fig. 9).--Sometimes a major physical change does not induce a corresponding change in vegetation. An example is the headwaters of Red Creek east of Flaming Gorge, where the intermittent stream channel appears to be much more deeply incised today than it was in 1870, and a deep roadcut has been put through the near slope. Yet the vegetation on the sagebrush flat across the valley (GCI = 62) and on the slope (GCI = 44) remains much the same, probably because the soil profiles were already drained. Big sagebrush and both low and rubber rabbitbrush are the dominant shrubs, with abundant needle-and-thread, western wheatgrass, Indian ricegrass and cheatgrass. Livestock use is evident. During the period, juniper trees underwent a decrease and then an increase in the channel area, and a small increase on the foreground and on the far slope [ARC: low fair; AT: stable].

Thus the area displays vegetative stability in spite of major physical change, probably because the essential growing conditions for the vegetation have not been altered. It is likely that these circumstances will continue indefinitely into the future.

Tower on Castle Rock (fig. 10).--In the absence o natural or artificial disturbance, it appears tha big sagebrush has the capacity to maintain itself within a community of poor ecological condition. The 1869 photograph of sagebrush just west of Castle Rock in Echo Canyon (fig. 3) shows a vigorous, dominant stand. It is reasonable to suppose that the dense shrubs suppressed herbaceous production in 1869, because they continue to do so today. Big sagebrush is by far the dominant shrub on the site, with scattered low rabbitbrush, bitterbrush (*Purshia tridentata*), ar wild rose (*Rosa woodsii*). Indian ricegrass is th principal grass, with infrequent bluebunch wheatgrass and Great Basin wildrye, and a general distribution of cheatgrass.

Site conditions have been such that several gullies have developed on the area, including on very deep drainage immediately in front of the photopoint. There is abundant sign of past and current heavy livestock use. Apparent range condition is low fair and apparent trend is downwar due to erosion (GCI = 59), but sagebrush remains very vigorous and stable and probably will continue to be so until disturbed to a significant degree.

From these examples of sagebrush stability it is possible to conclude first that big sagebrush wa an important plant dominant of late 19th century Rocky Mountain rangeland, second that the shrub represents a genuine climax for these sites, and third that the use and management of the past 11 years have not significantly altered that status

Sagebrush Increase or Establishment

That big sagebrush has increased markedly as a result of abusive land use is a near-axiom in th ecological history of the sagebrush zone. There is no doubt that such land use has taken place o that sagebrush has increased in distribution or density in some areas. The Jackson photo compar isons contain examples of apparent sagebrush increase or establishment as a response to site conditions of the past decades.

Wahsatch, Utah (fig. 11).--In 1869 a grassy mea with scattered shrubs (probably gray horsebrush [*Tetradymia canescens*]) surrounded old Wahsatch Station on the Utah-Wyoming border. In the time since, the meadow shows signs of intense early

use, probably as a result of livestock shipments from the station. In addition, the area was affected greatly by major construction associated with the station, railroad, and highway. These impacts are indicated by the advance of now-mature sagebrush into the meadow. With abandonment of the station these uses abated; subsequent use allowed establishment of a dense sward (GCI = 85) which excluded further sagebrush invasion. The meadow is now dominated by western wheatgrass and alkali bluegrass (Poa juncifolia), with some prairie junegrass, bluebunch wheatgrass, needle-and-thread, Great Basin wildrye, and numerous forbs. There is little sign of grazing use.

Under current management trends, Wahsatch Station will likely continue as a stable meadow excluding further sagebrush increase and even reducing the existing population as the shrubs expire [ARC: high good; AT: upward].

Fort Fetterman (fig. 12).--Ecological changes leading to an increase in sagebrush can be traced to probable grazing mismanagement on some sites. In 1870 Fort Fetterman on the North Platte River was sited on shortgrass prairie with a slight shrub presence, probably Wyoming big sagebrush (A.t. ssp. wyomingensis). In the decades since, a significant increase in sagebrush has occurred, probably initiated by animal concentrations associated with the military post and continued by heavy livestock grazing after the fort was abandoned. The herbaceous understory is now very patchy and hummocky blue grama (Bouteloua gracilis) and threadleaf sedge (Carex filifolia) in low production (GCI = 59). A general distribution of cheatgrass and absence of forbs indicate sheep range. Unless there is some disturbance of the site, it is likely to remain a degraded big sagebrush stand for some time to come [ARC: poor to low fair; AT: downward].

Camp on Blacks Fork (fig. 13).--Blacks Fork in southwestern Wyoming is a desert stream which at this point in 1870 was supporting a grassy meadow lined by trees and shrubs. In the years since, a shrub type developed (GCI = 53), dominated by big sagebrush with some rubber rabbitbrush and occasional black greasewood (Sarcobatus vermiculatus). Grasses still evident in scattered clumps include western wheatgrass, alkali sacaton (Sporobolus airoides), inland saltgrass (Distichlis stricta), and bottlebrush squirreltail (Sitanion hystrix), with some Kentucky bluegrass (Poa pratensis) and Great Basin wildrye in the protection of shrubs. Forbs are mostly weedy annuals. The riparian shrubs are now reduced to a few decadent stems of narrowleaf cottonwood (Populus angustifolia) and silver buffaloberry (Shepherdia argentea) with no reproduction.

These changes are likely due to impoundments and diversions of water upstream, which have lowered the water table and drained the meadow. In addition, because desert streams are oases, the meadow has likely undergone heavy livestock and wildlife utilization. These trends will probably continue to make the meadow warmer and drier than it was in Jackson's time [ARC: poor; AT: downward].

Summit of Black Hills (fig. 14).--Sometimes an increase in big sagebrush occurs as an unintended result of other management programs. Shortgrass plains vegetation similar to that in the 1869 view normally is found on the Laramie Mountains (referred to as the Black Hills in Jackson's time) in southeastern Wyoming. The major visual change in the scene is the establishment of limber pine (Pinus flexilis) and big sagebrush on slopes and in swales having increased snow accumulation. The change is due at least in part to the early use of fences to protect grade cuts from blowing snow. The fences lasted a long time (materials can still be found on the ground), and it is likely they improved site water relations sufficiently to allow shrub and tree development. Now the trees are acting as their own snowfence, continuing the change. An excellent herbaceous understory (GCI = 76) now includes western wheatgrass, needle-and-thread, bluebunch wheatgrass, prairie junegrass (Koelaria cristata), fringed sagewort, and western yarrow (Achillea millefolium). The new community appears very stable, and most likely will continue to slowly expand [ARC: good; AT: stable].

Atlantic City, South Pass (fig. 15).--The increase in big sagebrush on some sites has no ready explanation. One example is the valley above Atlantic City near South Pass, dominated in 1870 by a willow flat (Salix spp.). Patches of quaking aspen (Populus tremuloides), indicated by the numerous snags and down wood, appear to have occupied most of the foreground at one time.

A great deal of change has taken place since 1870, primarily through dredging of the river and road construction. These operations drained the willow flat sufficiently to allow the establishment of conifers. Secondary succession since 1870 has produced a mature stand of aspen. Concurrently, big sagebrush has increased in density substantially, on both the immediate foreground and the distant slope at right center, in response to an unclear ecological impetus. Whatever the reason, big sagebrush has clearly expanded its presence, and now forms a stable community (GCI = 68), with bitterbrush and Idaho fescue (Festuca idahoensis) as dominants [ARC: low good; AT: stable].

Sagebrush Combination Effects

As might be expected, the ecological changes affecting sagebrush density and distribution are not monodirectional on many sites. Various combinations of decrease, increase, and stability can be found, illustrating the hazards of making too-wide assertions about cause and effect in the big sagebrush ecosystem. The dynamic integration of site conditions and land management must be included in the appraisal.

Camp on the Box Elder (fig. 16).--Opposite trends in ecological change have taken place on the Box Elder drainage in central Wyoming. The 1870 view shows a uniform sagebrush-grass community of moderate shrub density. Today the entire bottomland has been put into cultivation, accompanied by an increase in trees. Only the foreground slope

resembles its former condition (GCI = 61), with Wyoming big sagebrush, winterfat (Ceratoides lanata), and yucca (Yucca glauca) the dominant shrubs. Major grasses are blue grama, threadleaf sedge, needle-and-thread, and prairie junegrass; fringed sagewort, prickly pear, and sunflower (Helianthus pumilus) are the most important of numerous forbs. Lower on the slope, black greasewood, rubber rabbitbrush, and fourwing saltbush occur in a blue grama-sedge sod. There is little sign of livestock use on the slope, and it has every evidence of long-term stability. Thus total change in the bottoms contrasts with stable uplands in the Box Elder drainage [ARC: high fair; AT: stable].

A Perpendicular Bluff (fig. 17).--The 1870 photograph of a sandstone bluff (across the canyon from the natural cave in fig. 8 shows a sagebrush-grass community on a sandy range site at the right and a salt shrub stand on the shale outwash slope at left. Today the sagebrush-grass stand remains stable, with big sagebrush, rubber rabbitbrush, sand dropseed, needle-and-thread, and Indian ricegrass as dominants. Shadscale and saltsage with scattered big sagebrush remain on the outwash slope but are much reduced, probably due to disease or insect predation on the short-lived salt shrubs. Bottlebrush squirreltail is now present on the slope in abundance. The swale bottom is still occupied by black greasewood. Stability and change are thus concurrent effects of site ecology, but big sagebrush has remained largely the same [ARC: fair (shale), good (sand); AT: stable].

Evanston Coal Mines (fig. 18).--Frequently the conditions for either sagebrush increase or decrease are attributable to an intensive local disturbance such as mining. For instance, the 1871 view of an Evanston coal mine shows a salt desert shrub community, likely saltsage and winterfat, already heavily influenced by land-disruptive activities associated with the mine and probably by unmanaged grazing as well. The near-certain consequence was that big sagebrush and rubber rabbitbrush assumed almost total control of the site. Only remnant saltsage and winterfat plants survived, with perennial herbaceous plants largely confined to protection of the shrubs. Short of major disruption of the shrubs, it was likely that this site would remain a big sagebrush stand in degraded condition [ARC: poor; AT: slightly downward].

Rapid industrial development of the surrounding area is now under way, resulting in destruction of the sagebrush stand and exposure of bare soil. The remaining sagebrush is as before, but will likely soon give way to development as well. At the same time the steep, rocky slope above the site (GCI = 61) continues to support a shrub-grass community, primarily big sagebrush and bluebunch wheatgrass, in high fair to good condition and stable trend. Thus conditions promoting increase, decrease, and stability of sagebrush have all occurred on this site.

Jackson Canyon (fig. 19).--The 1870 view of a rough cleft in Casper Mountain shows a stable, well-vegetated, intermittent stream channel. The canyon slopes apparently were burned some years previously, replaced in secondary succession by shrubs. Flood flows in the years following have greatly increased deposition of coarse material downstream. The coarse sediments are now dominated by dense silver sagebrush (Artemisia cana). Shrub cover on the uplands is mainly true mountain mahogany (Cercocarpus montanus), with skunkbush, big sagebrush, bitterbrush, and black sagebrush (Artemisia nova). Herbaceous vegetation is primarily bluebunch wheatgrass, prairie junegrass and threadleaf sedge, with a variety of forbs (GCI = 73). Cheatgrass generally infests the bottomland, probably due to heavy human and livestock use plus the effects of floods. A general compound of both ecological change and stability in sagebrush is evident here [ARC: fair; AT: downward (outwash)].

Portneuf Canyon (fig. 20 and 21).--All of the responses of sagebrush to the use and management of the past 100 plus years can be seen in the modern comparison with Jackson's 1872 views of Portneuf Canyon in Idaho. Big sagebrush has been removed in agricultural development of the stream bottom, together with construction of highway and railway lines. It has also given way to dryland wheat farming on the distant ridges, to construction of an interstate highway, to a limestone quarry, and to urban development (Inkom). The sum of all these influences equals a clear reduction of sagebrush distribution in the canyon.

On the bench in the left foreground of figure 20, however, it appears that sagebrush has increased in size and density, possibly as a result of grazing management. Range condition appears to be in low fair condition, although litter contributed by annual species is high (GCI = 76). Major grasses are Sandberg bluegrass (Poa secunda) and bluebunch wheatgrass with general cheatgrass.

At the same time, it is probable that little change has occurred on the basaltic plateau in the center distance because it is far too rough and broken for the plow and unsuitable to extensive livestock grazing. Except for the increase of juniper, it gives every evidence of site stability. Big sagebrush is by far the dominant shrub, with bitterbrush, skunkbush, and rubber rabbitbrush. Sandberg bluegrass and bluebunch wheatgrass dominate the drier ridges, while Kentucky bluegrass and western wheatgrass are found in the run-in areas. Ground cover is high (GCI = 81 with bare lava rock accounting for 38 points) [ARC: good; AT: stable (plateau)].

Thus at one location, decrease, increase, and stability of big sagebrush can be observed, with each response dictated by the particular combination of environmental factors in operation at that point.

DISCUSSION AND CONCLUSIONS

The Jackson photo comparisons contribute clear evidence toward understanding the ecological history of Rocky Mountain sagebrush rangeland since settlement. As a whole, they lend credence to the following observations:

1. Big sagebrush has a highly site-specific reaction to the use and management imposed on it during European settlement. Whether sagebrush increases, decreases, or remains stable is a function of both the kind of use and site characteristics.

2. There is little doubt that shifts in composition and relative density of both herbaceous and woody species have taken place on most sites. There is no means of assessing the relative magnitude of such changes, however. Based on general and circumstantial evidence alone, it is highly likely that a spectrum of change has occurred, again as a function of kind of use and site characteristics. That spectrum will range from virtually no change to total change, that is, entire replacement of native vegetation.

3. While it is clear that changes in sagebrush density have occurred, it is equally clear that there has been no major shift in sagebrush distribution as a result of use. The Jackson photographs provide evidence for the basic stability of rangeland types: grassland remains grassland, shrub stands retain their outlines, and low potential sites remain so. Only where extensive disturbance has taken place, and not always even then, can sagebrush be found today where it was absent in Jackson's time.

4. In macroterms, the appearance of the landscape today is a fair indication of its presettlement appearance. There is no basis for assuming that much of the big sagebrush distribution is a disclimax or a seral stage toward grassland. The photos support those who assert overall stability in sagebrush rangeland.

Thus it seems that a fair summary of the effects of use and management over the last 115+ years on Rocky Mountain sagebrush rangeland would be that although major change has occurred locally through the direct intervention of man, in any regional or broad-scale definition the sagebrush type remains essentially the same. In following the trail of Jackson, one must conclude that sagebrush <u>is</u> where sagebrush <u>was</u>.

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1985

SE

1872

USGS 148

Figure 2.--View of the Wasatch Mountains now in urban Salt Lake City.

1984

N

1869

USGS 2(

Figure 3.--Castle Rocks at the head of Echo Canyon, UT.

1985

SW

1871

USGS 54

Figure 4.--Camp on Gooseberry Creek in southern Idaho.

1985

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1869

USGS 765

Figure 5.--Death Rock at the mouth of Echo Canyon, site of Echo City, UT.

1978

NE

1870

USGS 291

Figure 6.--Granite ridges off the Sweetwater River in central Wyoming.

1978

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1870

USGS 308

Figure7.--Badlands on Blacks Fork, now called Church Buttes,
in southwestern Wyoming.

1984

W

1870

USGS 330

Figure 8.--Sandstone cave near confluence of Henrys Fork and Green River, now Flaming Gorge Reservoir, UT.

1978

NE

1870

USGS 335

Figure 9.--Headwaters of Red Creek east of Flaming Gorge Reservoir, UT.

1985

NE

1869

USGS 812

Figure 10.--Tower on Castle Rocks in Echo Canyon, UT.

1985

N

1869

USGS 2

Figure 11.--Site of old Wahsatch Station near the Utah-Wyoming border.

1977

NW

1870

USGS 256

Figure 12.--Site of Fort Fetterman on the North Platte River, central Wyoming.

1978

SW

1870

USGS 30!

Figure 13.--Camp on Blacks Fork near Church Buttes in southwestern Wyoming.

1978

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1869

USGS 837

Figure 14.--Summit of Black Hills near Laramie, WY.

1979

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USGS 302

Figure 15.--Atlantic City, near South Pass, WY.

1977

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1870

USGS 270

Figure 16.--Camp on the Box Elder in central Wyoming.

1984

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1870

USGS 331

Figure 17.--Perpendicular bluff near Flaming Gorge, UT (see fig. 8).

1985

1976

N

1871

USGS 128

Figure 18.--Evanston coal mines, Evanston, WY.

1977

SE

1870

USGS 869

Figure 19.--Jackson Canyon in the Casper Mountains, WY.

1985

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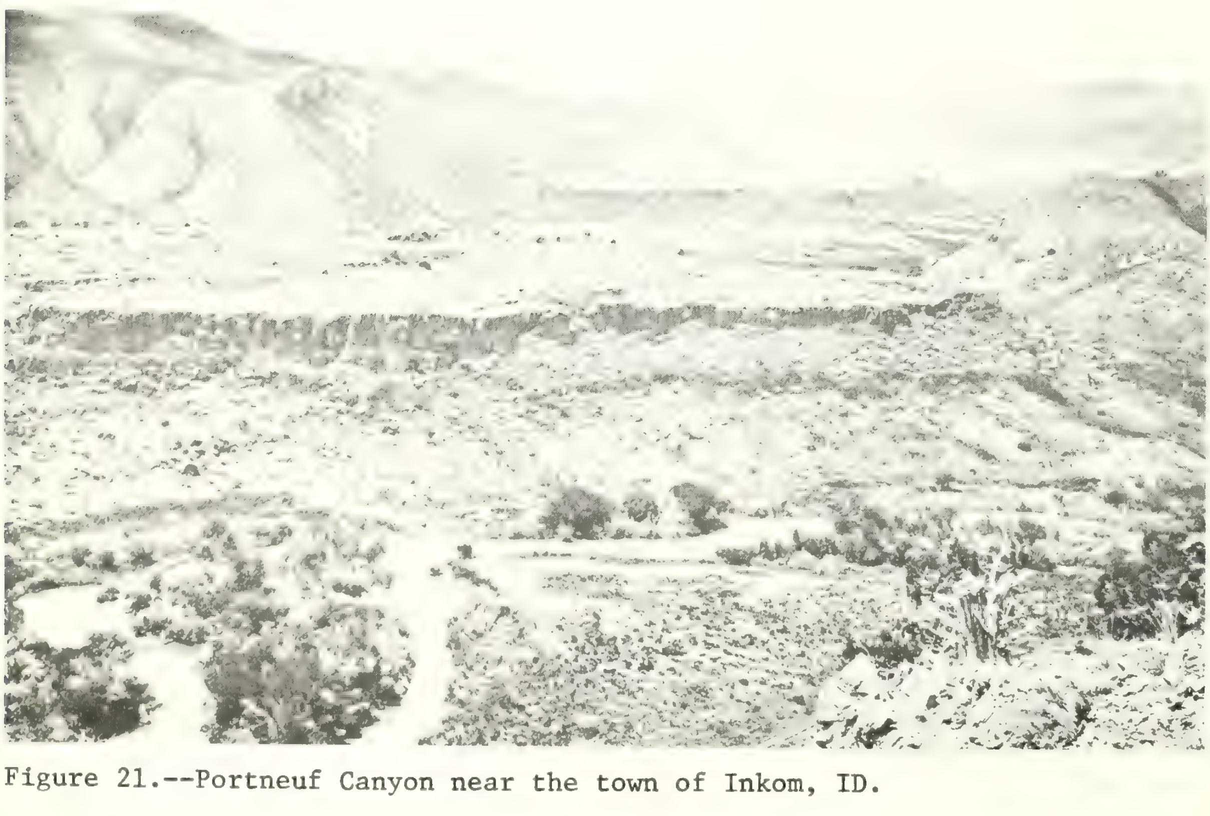
1872

USGS 155A

Figure 20.--Portneuf Canyon near the town of Inkom, ID.

1985



NW

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USGS 157

Figure 21.--Portneuf Canyon near the town of Inkom, ID.

COMPARATIVE LEAF ANATOMY OF SAGEBRUSH: ECOLOGICAL CONSIDERATIONS

Leila M. Shultz

ABSTRACT: Measures of leaf anatomy are compared with environmental parameters in examining the degree to which sagebrush leaf structure is adaptive. Specimens examined [all members of Artemisia L. subgenus Tridentatae (Beetle) McArthur] are ranked numerically according to habitat aridity gradient and analyzed for trends in anatomical structure according to that gradient. Field-collected specimens are compared to collections from a uniform experimental garden in order to segregate environmentally plastic variation from that which is inherited. Genetically controlled anatomical variation occurs among species in palisade length:width ratios, epidermal thickness, relative volumes of air space, palisade, parenchyma, and relative volumes of xylem. The Xeromorphy Index is a measure of the relative amount of water-conducting tissue in the leaf and reflects the degree of adaption of a species to water stress. Multiple regression analysis shows how various aspects of anatomical structure and leaf morphology may be used in a predictive model relating leaf structure to habitat.

INTRODUCTION

Few studies have addressed ecological or functional aspects of leaf anatomy, largely because of the difficulty of dealing with this morphologically and anatomically most variable of plant organs. Since Haberlandt's (1924) early and largely speculative work on physiological plant anatomy, few studies have directly addressed functional aspects of leaf anatomy. Shields (1950) reviewed earlier works which dealt with leaf xeromorphy and structural influences. Since 1950, ecological studies of leaf anatomy have been limited to descriptions of general trends in xeromorphy and even these have been few. They exist primarily in the work of Philpott (1961), Pykko (1966), Mortenson (1973), and Bocher (1979). The lack of supporting physiological data hinders the consideration of anatomical structure in a functional context.

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Because the information in this paper would be enhanced by companion physiological studies, much of the discussion is meant to stimulate that interaction and further study. To date, little effort has been made to correlate anatomical structure with habitat gradient or with physiology. This is due in part to the difficulty in quantifying anatomical structure. While quantitative microscopic methods have long been available, they have been largely ignored in the study of leaf anatomy. This study diverges from other descriptive ecological studies in the adoption of methods of quantitative anatomical measurement.

In spite of the predominance and ecological importance of sagebrush in western North America (fig. 1), structural studies of this shrub are practically nonexistent.

Figure 1.--Map of western North America showing the collective range for all members of Artemisia subgenus Tridentatae.

Previous work in leaf anatomy of Artemisia is limited to the developmental and morphological study of one species, A. tridentata Nutt. by Diettert (1937). The dissertation of Shultz (1983b) provides the first report of leaf anatomy for the 15 other taxa in the sagebrush complex. Two studies in wood anatomy address the ecological significance of structure. Moss (1940) reports the presence and discusses the significance of interxylary cork in stems of sagebrush, and Carlquist (1966) reports data that indicate that there is little variation among species in wood structure. However, the species possess a general pattern which is adaptive to desert habitats.

The principal questions addressed in this study are: (1) What is the range of variation in sagebrush leaf structure; (2) what aspects of leaf anatomy are genetically controlled rather than environmentally modified; and (3) how does anatomical structure correlate with ecological parameters? A related question, but one not explored in this paper, concerns those anatomical structures which show a phylogenetic rather than an ecological distribution. This topic is covered in Shultz (1983b). Patterns of leaf structure discussed here do show taxonomic patterns and may be used to define populations at the level of subspecies.

METHODS

Sampling

Collections for anatomical preparation were made of all sagebrush taxa, in the field, during late summer and fall of 1980, 1981, and 1982. Experimental garden collections were made from the University of Wyoming experimental sagebrush garden established by Alan Beetle. Sixteen of the eighteen taxa of sagebrush have been grown there under uniform environmental conditions. This experimental garden material provided a base of comparison in determining whether certain anatomical structures are environmentally induced or genetically controlled. Detailed measurements are based on those attributes which differ insignificantly between field and garden collections, and are presumably under genetic control.

Mature, late-season leaves were taken from vegetative shoots and fixed in the field. A total of 84 populations were sampled, with leaf sections prepared for microscopic study. Twenty-two collections were selected for intensive anatomical measurement. All anatomical material is vouchered with herbarium specimens and anatomical slides deposited at the herbaria of Utah State University (UTC) and Rancho Santa Ana Botanic Garden (RSA).

Microtechnique

Leaf sections are from mature, late-season leaves fixed in FPA (5 parts formalin: 5 parts glacial acetic acid: 90 parts 70 percent ethyl alcohol). Entire shoots were pickled in order to determine relative age and position of leaves examined.

Leaves were dehydrated through a tertiary butyl alcohol series and embedded in a high melting-point paraffin. Leaf sections were cut from a rotary microtome at 10-12 micron thickness. Longitudinal (paradermal) sections and transections were stained with safranin and fast-green, and prepared according to standard microtechnique (Johansen 1940). All measurements are from a high-resolution Leitz compound microscope, at 100 to 400X.

Fiber macerations are from leaves soaked in nitric acid for 24 hours at 58 °C and stained with safranin. Figures for fiber length represent average lengths; all fibers in a leaf were counted.

Scanning electron micrographs are from leaves fixed in glutaraldehyde, dehydrated through an alcohol-freon series, critical-point freeze-dried, and sputter-coated with gold paladium.

Morphometric Analysis

Several measurements are presented here for their utility in defining anatomical adaptions to xeric habitats. The Xeromorphy Index (Shultz 1983a, 1983b) is a measure of relative amounts of water-conducting tissue (xylem) within a leaf. Measurements are from leaf sections cut at 10-12 um. The area occupied by the xylem is calculated geometrically and measured in proportion to all other leaf tissue. The Xeromorphy Index (X) is calculated by dividing the area of the leaf transection (T) by the total vessel area (V), figured in mm^2. V is calculated by sampling 60 vessels in each transection and calculating an average diameter, figuring area as $2\pi r^2$ then multiplying that figure by the total number of vessels in the leaf. This was calculated by projecting the transection onto graph paper and calculating area by squares occupied.

The ratio expressed as "X" remains constant regardless of the position of the section within the leaf and therefore may be calculated from any point in the leaf. The formula calculated relative amount of xylem in the leaf. The higher the Xeromorphy Index (X), the less the amount of conductive tissue in the leaf.

Tissue volumes are figured from a point-intercept sampling method that was devised for this study. The calculation of volumes of palisade, air space, veins (includes xylem, phloem, and accompanying tissues), and water-storing parenchyma (bundle sheaths and their continuations) is modeled from a random sampling technique reported by Parkhurst (1982). Rather than measure from photographs, I took measures directly through the ocular microscope and increased the sample number. Ninety randomized dots were plotted on a grid micrometer. The dots were counted directly from the leaf section, with intercept counts recorded at five different positions in each leaf, providing a random sample of leaf tissues.

Table 1.--Morphological and anatomical data for Artemisia collections

Artemisia species	Collection[1] number	Habitat[2] type	Average[3] vessel diameter (μm)	Average leaf area (cm^2)	Xeromorphy[4] Index	Epidermal thickness (μm)	Palisade length/ width	%Palisade volume	%Air volume	%Bundle sheath
arbuscula ssp. arbuscula	4510	x	5.5	.28	217	4.0	3.2	47	9	33
arbuscula ssp. longiloba	4460	sx	4.5	.08	102	6.0	3.0	53	7	30
cana ssp. bolanderi	5680	sx	5.7	.37	128	3.5	3.0	51	25	30
cana ssp. cana	5451[5]	m	11.3	.20	111	10.3	4.0	54	14	30
cana ssp. viscidula	5421[5]	sx	6.9	.65	141	5.7	3.4	64	8	22
cana ssp. viscidula	4500	sx	8.7	.80	85	4.8	3.6	62	16	18
nova	4595	x	4.4	.09	186	5.7	2.3	39	11	35
nova	4557	x	5.4	.10	205	5.5	2.0	48	5	35
pygmaea	4560	xx	4.2	.01	514	8.5	2.1	71	5	14
pygmaea	4576	xx	3.6	.03	496	11.5	2.2	71	5	23
rigida	St. John s.n.	x	5.4	.09	190	4.8	2.8	60	6	34
rothrockii	4707	x	7.6	.29	249	8.5	2.2	41	21	28
rothrockii	5669	x	7.0	.34	250	6.0	2.1	64	11	15
spiciformis	5715[5]	sx	6.8	.65	144	3.2	2.8	49	19	28
tridentata ssp. parishii	4600	sx	7.2	.15	110	3.0	2.5	44	3	36
tridentata ssp. tridentata	5272	sx	7.0	.45	165	2.8	2.8	37	15	25
tridentata ssp. vaseyana	5474	sx	7.1	.60	73	2.8	2.8	46	17	33
tridentata ssp. vaseyana	5456[5]	sx	6.8	1.23	80	4.5	3.1	39	24	22
tridentata ssp. wyomingensis	5463[5]	x	6.7	.26	200	4.0	2.0	42	6	40
tridentata ssp. wyomingensis	McArthur U-80	x	6.3	.75	290	6.8	2.3	55	5	30
tripartita ssp. rupicola	5439	x	6.5	.48	201	4.5	2.8	53	9	27
tripartita ssp. tripartita	5461[5]	sx	8.4	.13	82	5.9	3.3	45	13	33

[1]Collection number: Shultz, unless otherwise noted. All collections at UTC.
[2]Habitat classifications: m = mesic, sx = semi-mesic, x = xeric, xx = extreme xeric.
[3]Average vessel diameter: average of 30 vessels, from primary veins.
[4]Xeromorphy Index: area of leaf-area of vessels (in transection).
[5]Samples from University of Wyoming - Uniform Experimental Garden.

Percent volumes are calculated from a sample of 450 point intercepts with the number of intercepts with different types of tissue calculated as a percentage of the whole leaf. Graphs are shown with lines for simple linear regressions and r^2 correlations. All graphs are from data summarized in table 1.

RESULTS

The habitat classification (table 2) is a qualitative ranking that is roughly based on patterns of precipitation, soil texture, and my field experience. Taxa are ranked within categories by increasing aridity. More information may be found in habitat descriptions presented in another paper in this symposium (Shultz 1985).

Table 2.--Sagebrush habitat classification

Species ranked in order of increasing aridity: m=mesic; sx=semi-xeric; x=xeric; xx=extreme xeric

Species	m	sx	x	xx
1. A. cana ssp. cana	x			
2. A. cana ssp. viscidula		x		
3. A. cana ssp. bolanderi		x		
4. A. tridentata ssp. vaseyana		x		
5. A. tripartita ssp. tripartita		x		
6. A. tridentata ssp. tridentata		x		
7. A. tripartita ssp. rupicola		x		
8. A. spiciformis		x		
9. A. arbuscula ssp. longiloba		x		
10. A. arbuscula ssp. thermopola		x		
11. A. tridentata ssp. parishii		x		
12. A. rothrockii			x	
13. A. arbuscula ssp. arbuscula			x	
14. A. rigida			x	
15. A. tridentata ssp. wyomingensis			x	
16. A. nova			x	
17. A. pygmaea				x

Qualitative and quantitative data for leaf morphology and anatomy of all species and subspecies of sagebrush (Artemisia subgenus Tridentatae [Beetle] McArthur) are presented for specimens collected from the field as well as from the uniform garden. Conclusions are drawn from aspects of anatomy that do not vary between the controlled and field conditions, or those structures that are apparently genetically controlled. Data for these measures are summarized in table 2.

Leaf Structure and Shape

Leaf architecture of the Artemisia tridentata complex fits a classic xeromorphic pattern in overall reduction in size, closely spaced veins, absence of spongy mesophyll, and a generally thick leaf lamina.

The basic anatomical pattern is illustrated in figures 2-5. Tissues are labeled in the schematic diagram of a leaf section shown in figure 6. The mesophyll of sagebrush leaves is composed entirely of palisade cells and lacks a spongy mesophyll. The xylem is composed entirely of vessels, with no tracheids. Fibers that accompany the veins are either gelatinous (in Artemisia rothrockii) or lignified (all other species). The prominent internal layer of non-photosynthetic parenchyma is the bundle sheath, with continuations and extensions. Resin ducts are present in all of the species and are associated with the veins and adjacent to the xylem. Leaf shape as well as the trend to size reduction in arid habitats are schematically shown in figure 7. All leaves have one central primary vein, two prominent lateral veins, and an intricate network of tertiary minor veins (figure 8).

Data for average leaf area are graphed with the habitat classification in figure 9. Leaves are entire (A. cana), pinnatifid (A. pygmaea), or three-lobed (all other species).

Leaves develop on lateral shoots with internodes shortened to the extent that the leaves are clustered into tight "buds". This arrangement is often referred to as a dolichoblast shoot. The leaves outermost in the cluster develop first. These leaves elongate rapidly in spring after overwintering and are termed "ephemeral" because they drop early in the spring and are easily identified by their unusually large size.

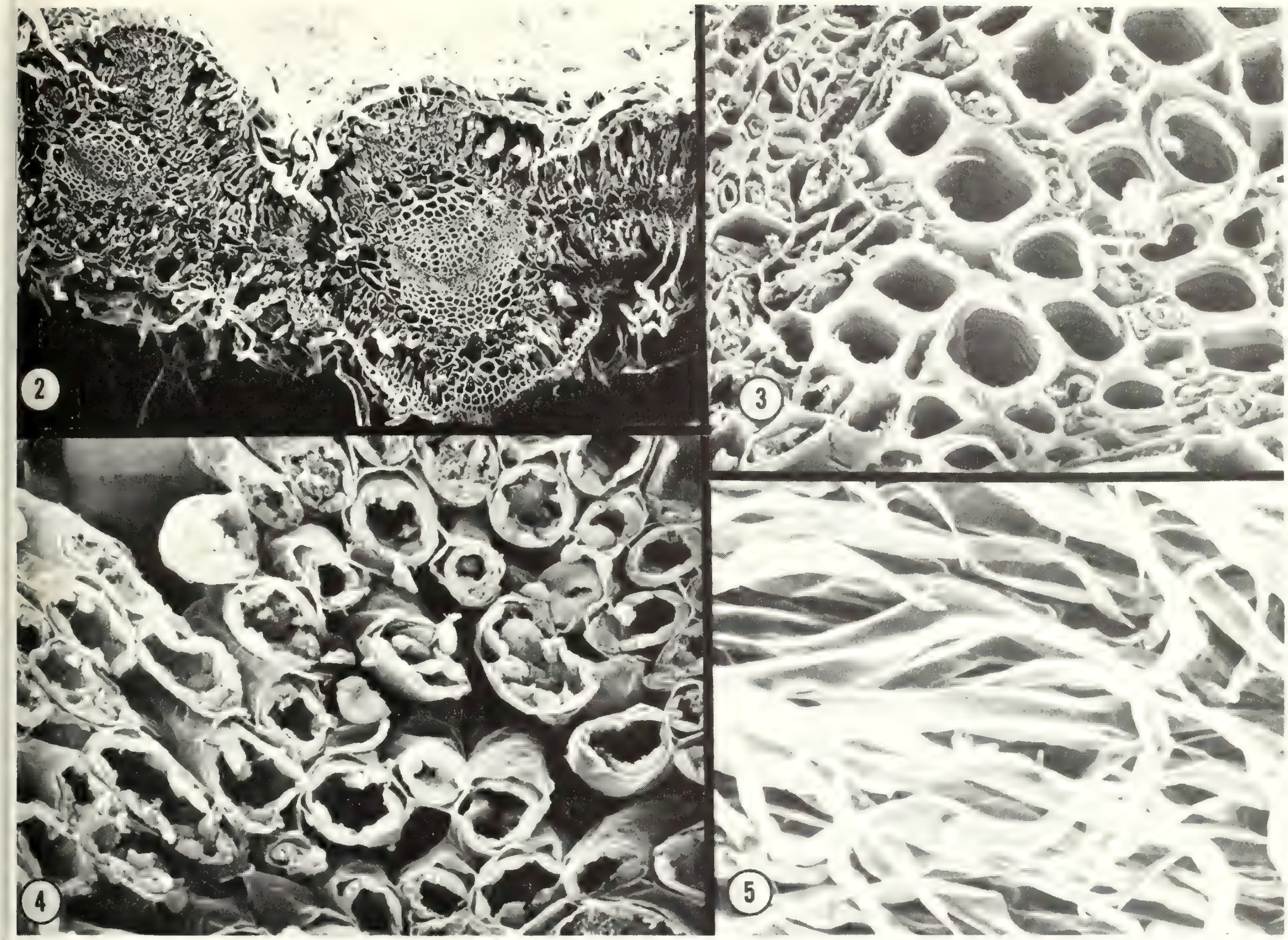
Species of sagebrush are either evergreen with leaves that remain photosynthetically active throughout the winter months, or deciduous after the plants have set seed. The drought-enduring evergreen species are Artemisia tridentata Nutt., A. arbuscula Nutt., A. nova A. Nels., A. pygmaea A. Gray, and A. rothrockii A. Gray. The deciduous, or drought-evading species are A. cana Pursh, A. tripartita Rydberg, and A. rigida (Nutt.) A. Gray.

Leaf hairs (trichomes) are either glandular or air-filled, T-shaped hairs (fig. 3).

The glandular hairs are biseriate, eight-celled, and contain the liquids that give sagebrush its characteristic odor. The T-shaped hairs are uniseriate, two-celled, and filled with air. The air-filled hairs form a dense cover on the leaf surface and are the cause of the silvery appearance of sagebrush.

Anatomical Measures

Xeromorphy Index.--Plants in the wettest habitats have more xylem per unit area than plants in the driest habitats. A high Xeromorphy Index indicates low relative volumes of xylem in the leaf. I devised this measure as a quantitative measure of xeromorphy. The Index shows a high correlation with habitat classification based on aridity (fig. 10).



Figures 2-5. Scanning electron photographs of Artemisia tridentata ssp. vaseyana (Shultz 4425). Figure 2.--Leaf cross-section with two of the three major veins, 140X. Figure 3.--Detail showing helically-thickened vessel walls, 1700X. Figure 4.--Detail of palisade cells. Note interconnecting plasmodesmatal strands, 1700X. Figure 5.--Detail of T-shaped hairs on leaf surface, 500X.

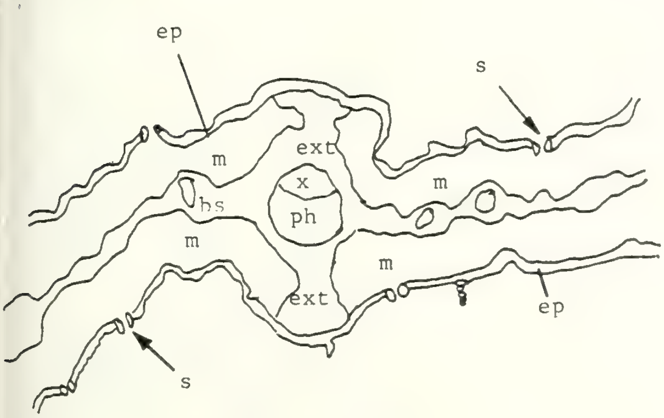


Figure 6.--Schematic diagram of typical sagebrush leaf section showing position of tissues: bs, bundle sheath; ep, epidermis; ext, bundle sheath extension; m, mesophyll (all palisade in sagebrush species); ph, phloem; s, stomatal pore; x, xylem.

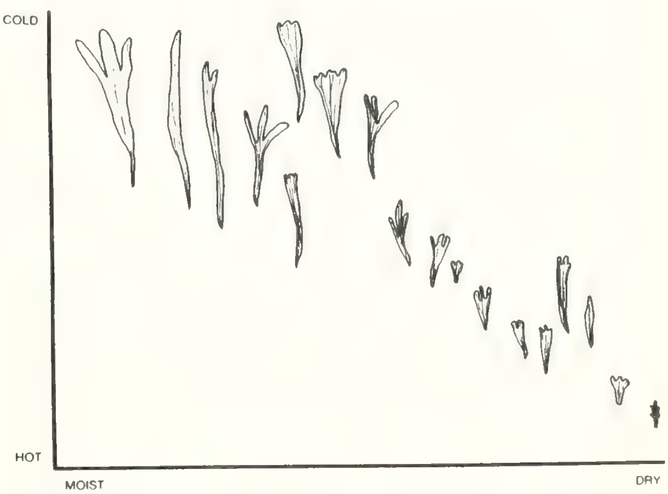


Figure 7.--Leaf morphology of Artemisia showing the trend for leaf reduction in progressing from cold, moist habitats, to hot, dry habitats. Each leaf represents one taxon within the sagebrush complex.

Stomates.--Stomates occur on both upper and lower surfaces and appear to be evenly distributed in most taxa. With the exception A. pygmaea, which has sunken stomates, guard cells are even with the plane of the epidermal wall. Where glandular trichomes are sunken in pits in the epidermal surface, stomates occur at the upper edge of the pit. Guard cells range from 8 to 14 microns wide and 15 to 25 microns long.

Schlerenchyma.--Schlerenchyma is present as fibers and as sclerified walls of the bundle sheath parenchyma. Counts of total fiber number and fiber lengths were made for a few leaves and lengths are presented in table 3.

Epidermal thickness.--Epidermal walls and their cuticles are generally thinnest in the species of mesic habitats. This relationship is shown by plotting average epidermal thickness against the xeromorphy index (fig. 11). Measures are from the area directly over the midvein, where there is no protective covering of hairs and the epidermis and cuticle are thickest. Measures range from 2.5 to 11.5 microns thick (table 2).

Air space volume.--Air space volumes range from 5 to 25 percent. Increasing amounts generally correlate with a decrease in palisade density.

Bundle sheath volume.--Bundle sheath parenchyma completely encircles each vein and forms continuations between all veins with extensions from major veins to the upper and lower epidermal surfaces. This results in a continuous sheet of water-storing tissues embedded within each leaf. Volumes range from 14 to 40 percent of total internal surface.

Volumes roughly increase in species along a continuum from dry to wet habitats, but show the closest correlation with changes in volume of palisade tissue (fig. 12).

Palisade cell length.--The longest palisade cells occur in the most mesomorphic species and the shortest in the most xeromorphic species. Th relationship of palisade length to habitat is shown in fig. 13.

Vein densities.--Vein densities range from an average 4.4 per millimeter to 14.3 per millimeter across the width of the leaf. This represents a greater density than reported for sun leaves of deciduous dicots (Wylie 1951) and is adaptation to aridity in that dense vascularization aids in maintaining even internal moisture balances.

Vessel area.--The difference in average vessel diameters among species corresponds to the habita gradient, with the the widest vessels found in th wettest habitat and the narrowest in the driest habitats. Relative volumes of vessels also decrease with aridity, as discussed in the explanation of the Xeromorphy Index (fig. 14). The percentage of space occupied by veins in the leaf (table 2) does not correspond to the area occupied by the individual vessels. Apparently, as xylem vessels decrease in diameter and number, there is a concurrent increase in other tissue within the veins such as interxylary parenchyma and fibers.

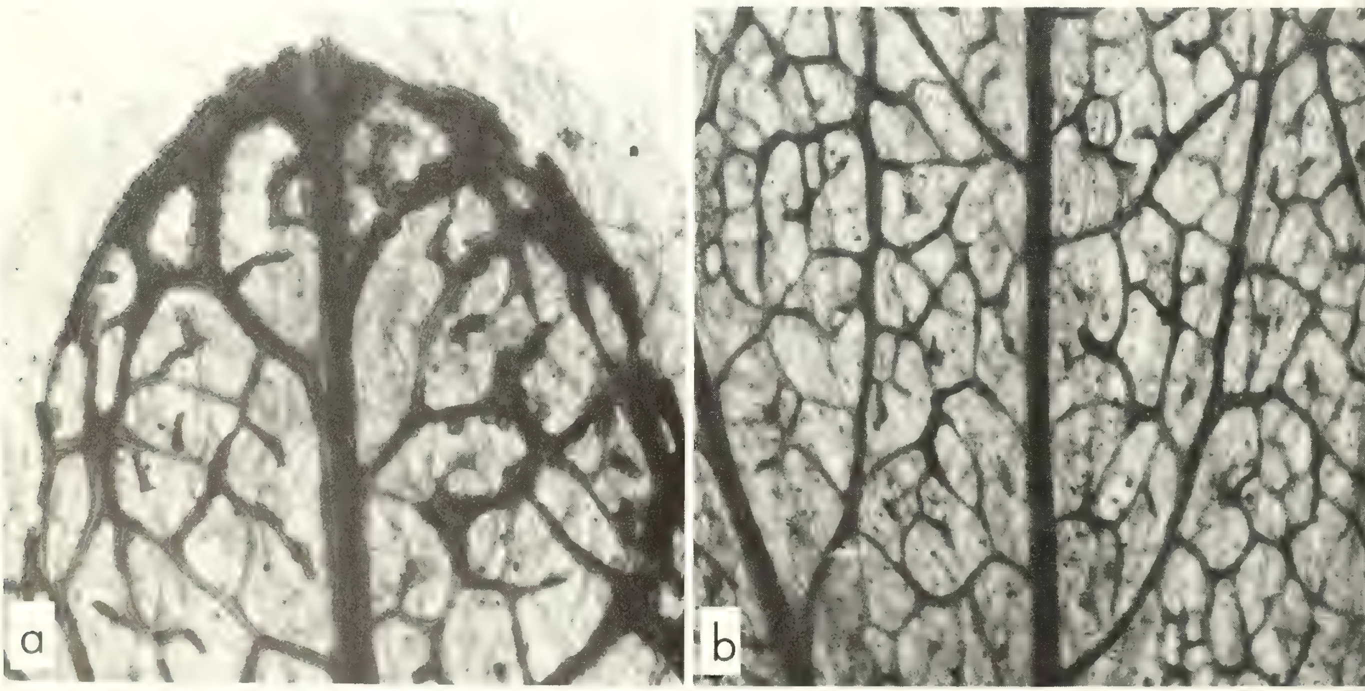
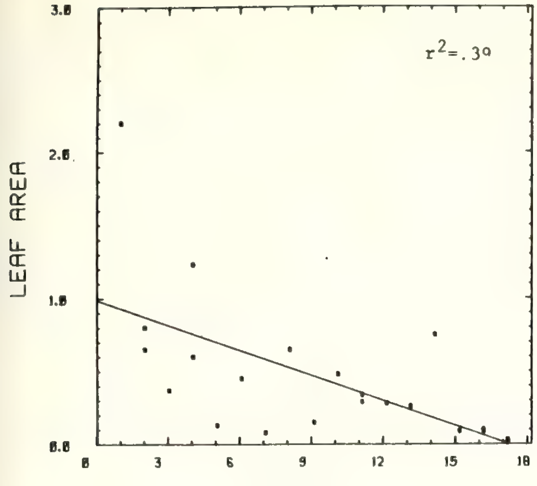


Figure 8.--Vein patterns of Artemisia tridentata ssp. vaseyana, from a leaf clearing. Figure 8a.--Terminal vein ending in one of the leaf lobes. Note hydathodal region at tip of vein and conspicuous sclerified bundle sheath cells. Figure 8b.--Shows central primary vein with secondary and tertiary veinlets.



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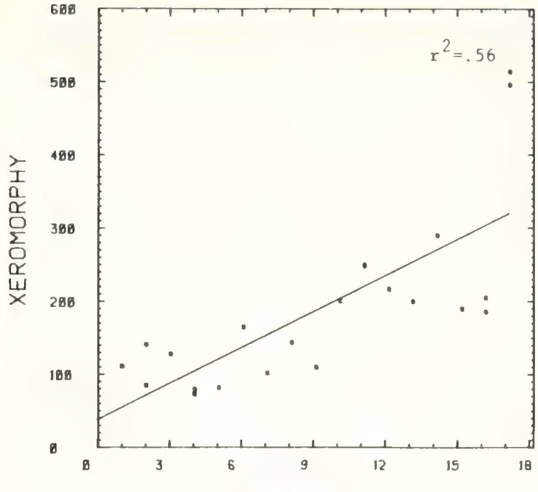

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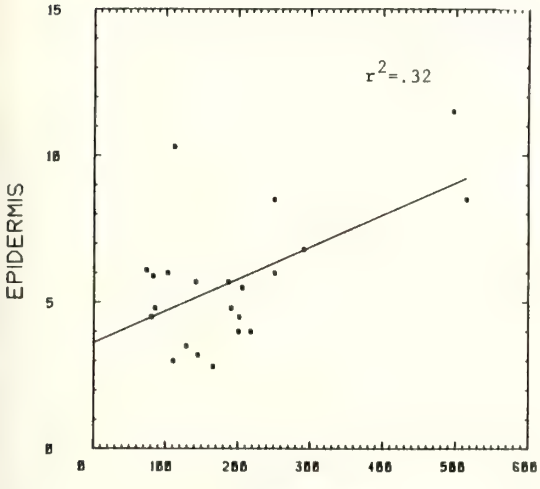

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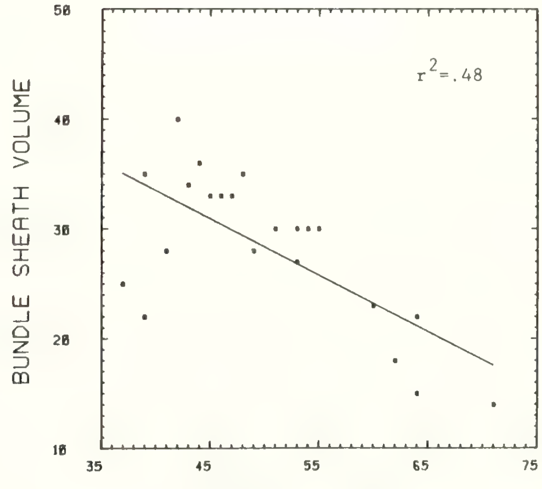

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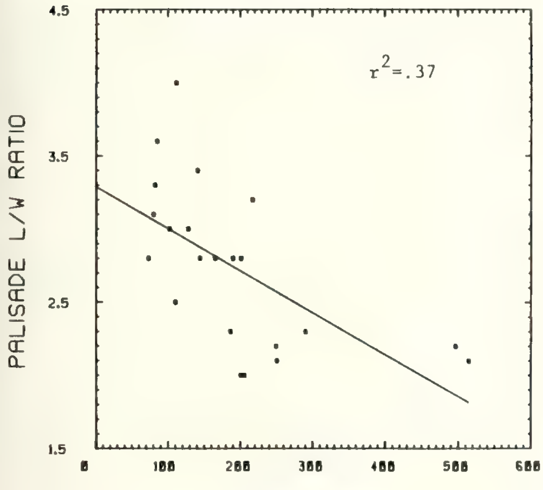

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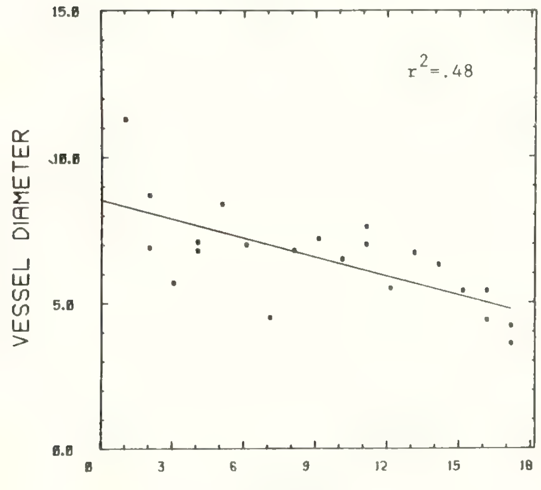

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Figures 9-14.--Correlations of anatomical data to various parameters, as indicated in the separate figures. All data are from table 2.

Figure 9.--Comparison of leaf area to habitat.
Figure 10.--Comparison of habitat to xeromorphy index (from tables 1 and 2).
Figure 11.--Comparison of Xeromorphy Index to epidermal thickness (from table 2).
Figure 12.--Comparison of palisade volume to bundle sheath volume (from table 2).
Figure 13.--Comparison of the Xeromorphy Index to the palisade l:w ratio (from table 2).
Figure 14.--Comparison of the habitat index (table 1) to average maximum vessel diameters (table 2).

DISCUSSION

Leaf structure is obviously correlated to plant habitats and thus plays a significant role in plant function. Figure 15 diagrammatically shows the relationship of leaf structure to physiological measures of water loss and provides a useful reference for the following discussion of leaf structure and function.

Because comparative physiological and ecological data are lacking for the species of sagebrush, I am limited to a discussion of ecological aspects of leaf anatomy in relation to general and rather crude patterns of habitat aridity. Ideally, the data presented in this study would be correlated with physiological data. While extensive studies have been made of *Artemisia tridentata* (Caldwell 1979), data are not available for other species of sagebrush. We know from the work of Caldwell and his associates that both stomatal resistances and water potentials are high in *Artemisia*, as expected for xeromorphic shrubs. Until physiological data are available for other species, this work will rest as a report of anatomical structure as it relates to general trends in environmental gradients.

The leaf arrangement as short clusters on leafy shoots may be adaptive in cold as well as dry environments in that the tight leaf clusters are self-insulating and provide protection from rapid temperature changes, from cold as well as from heat. The shading effect of overlapping leaves may be especially important in the summer time and provides protection to developing leaf primordia. Leaf hairs are among the first structures differentiated from the leaf primordia and both glandular and air-filled hairs cushion and surround the layers of leaves in the fascicle. Protective features of leaf hairs are thus available during rapid meristematic growth.

The ecological significance of hairs on leaf surfaces varies according to type of hair as well

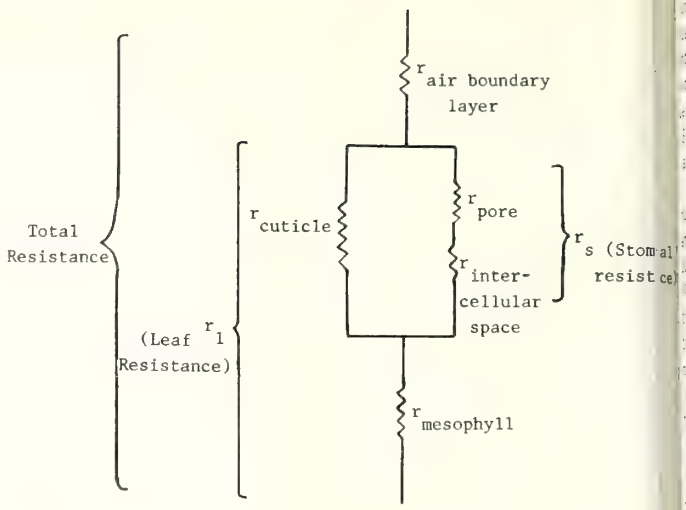

Figure 15.--Model of total leaf resistance to water loss showing roles played by various structures within the leaf (redrawn from Kramer 1983).

as varying between species. Studies of *Encelia* indicate that the importance of pubescence is in modifying the heat load of the plant. Hairs increase light reflectance which in turn regulates leaf temperature at a thermal optimum for photosynthesis (Ehleringer and others 1976; Ehleringer and Mooney 1978).

In *Encelia*, hairs are simple and there is no stal[k] as in the T-shaped hairs of *Artemisia*. The elevated hair layer in *Artemisia* T-shape creates dead air space next to the epidermal surface and the dense cover of hairs extends the leafy boundary layer as well as reducing heat load by increasing light reflectance. Thus, the T-shaped hairs of *Artemisia* probably function in reducing transpiration by trapping air and raising relativ[e] humidity of the leaf surface as well as

Table 3.--Fiber length and abundance

Taxon (Artemisia)	Collection	Leaf Length	Fiber Length	Fiber No.
A. arbuscula ssp. *arbuscula*	Shultz 4510	12 mm	575 um	108
A. arbuscula ssp. *longiloba*	Shultz 4460	5 mm	289 um	67
A. cana ssp. *viscidula*	Shultz 4508	12 mm	727 um	53
A. nova	Shultz 4550	10 mm	531 um	88
A. pygmaea	Shultz 4560	4 mm	370 um	1400
A. rigida	St. John s.n.	n.a.	738 um	630
A. rothrockii	Shultz 4706	7 mm	677 um	198
A. tridentata ssp. *parishii*	Shultz 4600	n.a.	857 um	40
A. tridentata ssp. *vaseyana*	Shultz 4442	7 mm	376 um	13
A. tripartita ssp. *tripartita*	Ballard 6	12 mm	396 um	31

functioning in reducing leaf temperature. Glandular hairs form the site of synthesis of anti-herbivore compounds that significantly contribute to the success of sagebrush. Gland cells exude monocyclic and acyclic monoterpenes (Stangl and Greger 1980) as well as sesquiterpene lactones (Kelsey and Shafizadeh 1980).

Microscopic differences in anatomical structure are closely correlated to the habitats in which different species and subspecies of sagebrush occur. Several measures are presented here for the utility in defining anatomical adaptations to xeric habitats. These difference are measured as: (1) variance in relative volumes of leaf tissue; (2) differences in leaf surface to volume ratios; (3) variance in leaf size; and (4) variance in amounts of water-conducting area in the leaf. These data are summarized in table 2. The discussion of anatomical variation deals with ecologically significant aspects of the variation.

The relationship of the Xeromorphy Index to habitat (fig. 10) suggests the physiologic importance of relative amounts of xylem in leaf tissue. The diminution of water-conducting tissue in increasingly arid habitats apparently provides a means of conserving water.

The individual water conduits, or vessels, vary in width and abundance according to habitat. The widest vessels in the sagebrush complex occur in the species of mesic habitats (Artemisia cana) and the narrowest in the most xeric habitats (A. pygmaea). For structural reasons, it is reasonable to assume that narrow vessels have a greater resistance to negative tensions in the water column and that wide vessels would be more likely to collapse from the pull of high negative water tensions. Negative water potentials of -70 bars have been reported for A. tridentata (Dina and Klikoff 1973) and presumably higher negative tensions would be found in species of drier habitats.

Although limited quantitative data are available, stomatal densities do not appear to be a sensitive indicator of environmental gradients among species of sagebrush. Stomatal densities do not vary greatly among the taxa, except for Artemisia pygmaea, which has approximately twice the stomatal density of other species. As expected from habitat and growth form, A. pygmaea also has the most xeromorphic leaf structure. The largest guard cells and pore openings are found in the polyploid species A. rothrockii, A. tridentata ssp. wyomingensis, and A. spiciformis (McArthur and Pope 1975; McArthur and others 1981). Larger pore openings would obviously compensate for lower stomatal densities, but these measures remain to be calculated when corresponding water relations data are made available.

Fiber length apparently correlates more with leaf length than with habitat parameters. Correlations here become circular, however, in that leaf length is somewhat relative to leaf size, which in turn correlates to habitat (figures 8 and 9). Fiber abundance dramatically increases with habitat aridity (table 3). The most mesomorphic species have the fewest fibers (Artemisia cana and A. tridentata ssp. vaseyana); the greatest number occur in the most xeromorphic taxon, A. pygmaea.

Transport and storage of water appears to be the major function of the bundle sheath. An internally embedded layer of water-storing and transporting tissue should be a considerable advantage in leaves where water is limited, and appears to be a very effective specialization in desert plants. Because the sheath separates veins from photosynthetic parenchyma (fig. 6), water must move through the sheath before reaching the mesophyll. The sheath continuations provide a route for movement of water--internally in the intervein connection, and outwardly in connection to the epidermis, a layer which also provides lateral water transport. Since the sheath parenchyma cells are all contiguous they inhibit air movement between upper and lower portions of the leaf. The simple pits between the cells allow the free exchange of water. Stomates occur on both upper and lower leaf surfaces and provide the means of gas exchange to the mesophyll above and below the water-storing parenchyma.

Storage of metabolites and waste products appears to be another function of the sheath parenchyma. The visible amount of material within the sheath increases during the growing season. Late season leaves show an especially high amount of stainable materials. Changing concentrations of sugars in the sheath cells is an effective means of making osmotic adjustment within the leaf.

The significance of differing relative volumes of airspace is not clear since there is no simple correlation with environmental gradients. Generally, the smallest air volumes and therefore the most densely packed palisade are found in plants growing in the driest habitats. However, species growing in extremely arid habitats occasionally have very high volumes of air space, such as Artemisia rothrockii. Other factors such as internal layers of cuticle and shapes of palisade cells should be considered in the evaluation of the internal water balances. An optically refractive layer surrounds the palisade cells of A. rothrockii. This is similar to the internal cuticular layers reported by Frey-Wyssling and Hauserman (1941), and would reduce water loss from palisade cells. This protection from water loss in well-aerated leaves would explain the unexpectedly high volumes of air space in A. rothrockii.

Species of Artemisia that are winter-deciduous generally have greater volumes of air space than the evergreens; the drought-enduring evergreens generally have a more densely packed palisade and lower volumes of air space. The significance of an internal aerating system has been explored by a number of workers. Turrell (1944) found that internal to external surface ratios and transpiration rates are positively correlated with the volume of intercellular air space. Schroder (1937) demonstrated that unwatered plants show a 30 to 52 percent decrease in intercellular air

space. Likewise, the lesser amounts of intercellular air space in evergreens (Nius 1931) may be a corollary of reduced air space in water-stressed plants. Low amounts of internal air may have a limiting effect on rates of CO_2 exchange. Mooney and Dunn (1970) observed that limitation of water loss by evergreens during periods of drought may result in reduction of the rate of CO_2 exchange between the ambient air and chloroplasts.

Physiological studies suggest that, for structural reasons, leaves with a mesophyll composed entirely of palisade have greater photosynthetic efficiency than leaves with spongy mesophyll. This is due to the maximal exposure of chloroplasts to light and carbon dioxide in the elongate palisade cells. Because of the large surface area of palisade, up to 1.6 to 3.5 times are great as that of spongy mesophyll (Turrell 1936), there is also a greater potential for water loss. Experimental studies show that water deficits as well as high light intensities contribute to increased development of palisade. Perhaps even though internal surfaces are increased, the overall reduction of external surface is of critical importance to plant water relations.

Table 4 shows the results of a multiple regression analysis in which habitat classification is compared to four variables: the Xeromorphy Index, volume of air space, epidermal thickness, and palisade length:width ratio. For reasons already discussed, one variable alone does not demonstrate leaf xeromorphy. However, these four aspects of leaf anatomy used in a model show greater than 85 percent correlation to habitat and may be used in predicting fitness of a leaf structure to arid habitats.

Table 4.--Regression analysis using habitat as the dependent variable

Range: 1-22

	Coefficient	Standard error
Constant	3.413	0.490
Xeromorphy index	9.999	.999
Leaf area index	-.308	.179
Percent air volume	-.013	.010
Epidermal thickness	-.030	.039
Palisade L/W ratio	-.358	.158
R-SQ.: 0.893	Corr. R-SQ.	0.860

SUMMARY

Leaves of Artemisia fit a xeromorphic pattern in a number of measures. Ecologically significant anatomical variation exists in the amount of palisade tissue, amount of water-storing parenchyma, degree of palisade packing, vessel diameters, and relative amounts of xylem within the leaf. With increasing aridity, compensation in leaf structure occurs in: (1) relative amounts of water-conducting tissue, expressed as a high Xeromorphy Index; (2) amount of air space or internal cuticular layers; (3) vessel diameter; (4) palisade length/width ratios, and (5) epidermal wall thickness. While there is not a precise linear correlation of habitat and trends within any one of these measures, that they act together as a leaf system is demonstrated by the high correlation of these five measures with habitat in a multiple regression analysis.

Inasmuch as quantitative measures of leaf structure fit within a model with a high predictive value for habitat aridity, we can assume that leaf structure and function are intimately related. The demonstration of how leaf tissues work together as a system is basic to an understanding of the relationship of leaf anatomy to physiology.

Sagebrush leaf structure exhibits considerable interspecific variation and is obviously well-adapted to arid habitats. The flexibility of the genetic program that governs this structure may explain to a large degree the rapid evolution and extensive colonization of sagebrush in the west.

Quantification of the habitat parameters and their correlation with anatomical structure provide information on the patterns of diversification of sagebrush and how these species have adapted to the cold deserts of the Great Basin. It is within this evolutionary context that we should continue to explore the relationship of plant structure and function.

ACKNOWLEDGMENTS

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SOME EDAPHIC AND COMPOSITIONAL CHARACTERISTICS OF ARTEMISIA TRIDENTATA AND ASSOCIATED PLANT COMMUNITIES IN SOUTHEASTERN UTAH

Kimball T. Harper and Richard A. Jaynes

ABSTRACT: The major plant communities of the Kaiparowits Plateau below the pinyon-juniper zone include mat saltbush, green molly-shadscale, shadscale-grass, grassland-mixed shrub, blackbrush, and sagebrush. The first three communities occur on the lower benches at about 4,265 ft (1 300 m) elevation and are separated by strong edaphic differences. The latter three communities occupy upper benchlands at 4,922 ft to 5,577 ft (1 500 to 1 700 m). Soil texture and chemistry are similar among these vegetational types, but soils are consistently deeper and less stony under grassland mixed-shrub vegetation. The distribution of blackbrush and sagebrush shows little correlation with either edaphic or microclimatic variables. Their distribution may be attributable to unequal ability of those species to reinvade after fires. Increasing site xericness was correlated with less vegetative cover and fewer species per unit area sampled. Shrubs and grasses showed marked differences in site preferences. Shrubs performed best on ridge crests and shallow soils, while grasses preferred bases of slopes and deeper, sandy textured soils.

INTRODUCTION

Abundant coal of low sulfur content occurs on the Colorado Plateau portions of Utah, Arizona, Colorado, and New Mexico. Power companies, required to meet more stringent standards for sulfur dioxide emissions from coal-powered electrical generating plants, have used progressively more coal from Colorado Plateau mines. Since much of the coal is extracted from open-pit mines, a major problem facing energy developers is stabilization of disturbed areas. Revegetation using adapted species is the most economical means of stabilizing mine wastes, but even after more than a decade of intensive revegetation research in the more arid sections of the Plateau, revegetation programs still do not always yield fully acceptable results. On sites where topsoil characteristics and topography have been significantly altered, land managers may not be able to use adjacent natural vegetation as a model of appropriate species combinations for reclamation. Better procedures are still needed for deciding which species to plant, how to plant them, and what the sustainable limits for plant cover are at any given site. Such knowledge would also help managers know whether a reestablished plant cover is approaching the potential for the site. Before such management problems can be resolved adequately, the natural ecology of each site must be understood.

Prior workers in the arid environments of the Colorado Plateau have identified edaphic and topographic factors that are influential in controlling the distribution of certain plant communities. Community types and soil-vegetation relationships in the shadscale zone of Grand County, UT, were investigated by West and Ibrahim (1967). They reported that edaphic discontinuities correlated well with vegetational changes. Gates and others (1956) found that soil factors, such as salinity and one-third atmosphere soil moisture, were significantly correlated with changes in some plant communities in the Great Basin.

In a study of grassland communities in northern Utah, Harner and Harper (1973) theorized that site mesicness increased from slope top to slope base positions as a result of differences in water infiltration. They suggested that ridgetops retain less moisture due to overland flow of precipitation. Midslope positions often receive roughly as much "run on" as runoff. Slope bases were considered to be more mesic than other positions due to more "run on" than runoff. They concluded that the relative contribution of perennial forbs and grasses increased as sites became more mesic. Loucks (1962) also found slope position to be a good index of available soil moisture in local situations.

Early revegetational research produced few techniques that would guarantee success in truly arid regions (Bleak and others 1965; Plummer and others 1968). Plummer (1966) noted that early rehabilitation plantings in the arid zone had been done on a "let's see what happens" basis.

Later workers recognized the need to more precisely identify environmental factors

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exerting the greatest influence on revegetation (National Academy of Sciences 1974). In the past decade, better procedures and plant materials have become available (Aldon 1978; Frischknecht and Ferguson 1979; McKell and others 1979), but much still remains to be done. A better understanding of the relationships between soils, topography, precipitation, and natural vegetations would substantially improve planning for reclamation projects (Hutchings 1966; Cook and others 1974; Alvarez and others 1974; Harper and others 1975).

Our purpose here is to describe the major plant communities below the pinyon-juniper zone on the Kaiparowits Plateau and to quantify their relationship to climatic, edaphic, and topographic variables. The results should clarify environmental-vegetational relationships in the area and help workers select more appropriate species for specific situations. We will illustrate how our results can be applied to increase success of revegetation projects in the area.

DESCRIPTION OF THE STUDY AREA

Vegetation and associated soils of the Kaiparowits Basin were sampled on upper and lower benchlands northeast of Glen Canyon City, Kane County, UT. Abrupt changes in elevation give a step-like aspect to topography in the study area. Soil parent material for the sandy loam upper benchland sites (ca. 5,085 ft [1 550 m]) is the Straight Cliffs sandstone formation with some localized influence from Mancos shale. Soils on the lower benchlands (ca. 4,363 ft [1 330 m]) range from clay soils derived from Tropic shale to sandy clay loams derived from Straight Cliffs or Dakota sandstones.

The study area is characterized by elements of both cold and warm desert vegetation adapted to approximately 8.7 inches (22 cm) of mean annual precipitation (fig. 1). Two precipitation peaks occur in most years: one in winter (January and February) and the other in July and August. Precipitation and temperature data were collected near Glen Canyon at 3,900 ft (1 189 m) elevation. Synoptic climatological patterns for the region of concern suggest that precipitation should average about 1.9 inches (4.8 cm) more per year on the upper as opposed to the lower benches. Long-term regional patterns also predict that annual temperatures will average about 1.3 °F (0.7 °C) lower on the upper benchland (Betancourt 1984).

METHODS

Twenty-four sites were studied in various plant communities on apparently undisturbed upper and lower benchland area. Where possible, sites were paired for contrasting exposures supporting broadly comparable vegetation and soil. At each site, three 0.05-acre (0.02-ha) stands were established along a topographic gradient with one stand at each of the top, middle, and basal slope positions. At each stand, exposure was measured

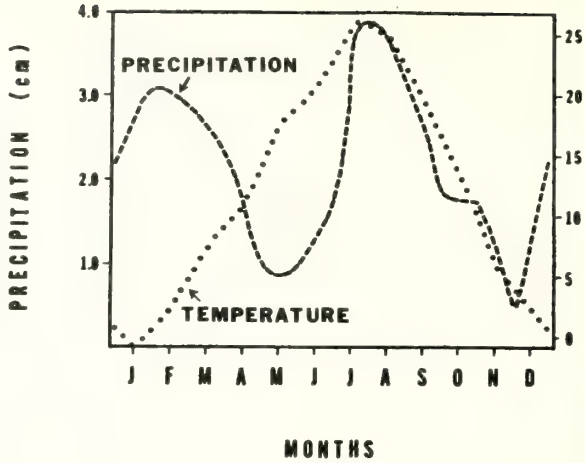


Figure 1.--Average precipitation and temperature at Glen Canyon City, Kane County, UT, for the period January-December 1972-75. Data supplied by Dr. B. W. Wood. Data collection was supported in part by Arizona Public Service Commission and California Edison Company.

in degrees from north and converted to an index of plant growth potential using a procedure described by Beers and others (1966). Their index utilizes potential solar radiation on a slope to approximate water and temperature stresses to organisms. The method assigns a value of zero to southwestern exposures and 2.0 to northeastern exposures: intermediate exposures receive values between zero and 2.0.

Vegetational data were collected at all stands during the period May 13-30, 1975. Twenty-five quadrats (each 2.7 ft^2 [0.25 m^2] in size) were spaced regularly over the surface of each stand. Data recorded for each quadrat included: (1) cover classes for living tissue, litter, and surface rocks larger than 0.16 $inches^2$ (1 cm^2) (Daubenmire 1968), (2) relative contribution of shrubs, perennial forbs, perennial grasses, and annuals to total living cover, and (3) presence for all vascular species.

Data recorded for each stand included a list of all species rooted therein, steepness of slope, and average soil depth from 20 random penetrometer readings. In addition, a composite soil sample was collected within each stand. The sample consisted of 12 cores (0.75 inch [1.9 cm] diameter and 6.0 inches [15 cm] deep) taken at regular intervals across the surface of the stand. Water infiltration rates (cm/min) were recorded at each site with ring infiltrometers. The infiltration rate for a stand was taken to be the average time required for disappearance of each of three successive 0.4-inch (1.0 cm) aliquots of water into initially dry soil. Percent rock is calculated as the average of percent rock cover (rocks >1 cm^2 [0.16 $inches^2$]) and rock content (diameter >2 mm [0.88 inch]) expressed as percent dry weight of the soil.

Independent	Dependent
Slope position (top=1, middle=2, bottom=3)	Percent total living cover
Exposure (Beers and others 1966 index)	Percent composition shrubs
Soil depth (cm)	Percent composition perennial forbs
Clay (percent)	Percent composition perennial grasses
Sand (percent)	Percent composition annuals
Percent rock	Average number species/quadrat
Slope steepness (percent)	
Infiltration rate (cm/min)	
Elevation (m)	
pH	
Salinity (ppm)	

A stepwise multiple regression procedure was used to provide predictive equations for various parameters of vegetation (Wikum and Wall 1974). The independent and dependent variables are above. Multiple regression provides an estimate of how various environmental factors interact to influence plant frequency and/or cover. The analyses were performed using data from our field samples and an arbitrary minimum F-value of 2.0 for admission of an independent variable to the analysis. The program terminated automatically when no remaining independent variable produced an F-value of 2.0 or more.

RESULTS

Community Characteristics

The communities differ in respect to soil texture, elevation, and soil salinity (table 1). The vegetative types can be conveniently grouped according to position in the landscape. Mat saltbush (*Atriplex corrugata*), green Molly (*Kochia americana*)-shadscale (*Atriplex confertifolia*), and shadscale-grass (primarily galleta [*Hilaria jamesii*], but also with considerable Indian ricegrass [*Oryzopsis hymenoides*]) occur on the lower benchlands. The upper benchlands support a mosaic pattern of the following three vegetative types: grassland-shrub (Indian ricegrass, galleta, sand dropseed [*Sporobolus cryptandrus*], blue gramagrass [*Bouteloua gracilis*], shadscale, matchweed [*Gutierrezia sarothrae*], and Brigham tea [*Ephedra torreyana*]); blackbrush (*Coleogyne*

Table 1.--General characteristics of environment and vegetation associated with the six vegetative types recognized. The standard deviation follows the mean for each value

No. of study sites	Mat saltbush 6	Green Molly/ shadscale 6	Shadscale/ grass 21	Grassland/ shrub 21	Blackbrush 12	Sagebrush 6
Abiotic characteristics						
Elevation (m)	1,308±5	1,279±3	1,335±26	1,522±47	1,583±65	1,659±5
Slope (percent)	6.8±5.0	3.5±2.3	8.5±5.6	4.0±2.2	5.7±2.7	4.7±4.0
Texture (percent)						
Sand	13.8±4.2	47.3±7.0	64.4±11.4	74.4±8.8	72.7±6.1	70.5±3.0
Silt	22.0±3.0	17.2±3.1	13.0±5.9	8.1±4.9	6.7±3.3	11.0±3.5
Clay	64.2±4.2	34.3±4.9	24.4±8.4	17.3±5.1	20.7±3.4	18.3±2.7
Ave. percent rock (>1 cm)	2.0±0.9	36.2±4.1	16.9±8.6	5.6±9.2	6.4±6.5	11.8±4.8
Ave. soil depth (cm)	49.5±16.4	17.7±4.4	31.7±14.7	46.7±21.6	22.2±14.9	19.2±4.9
Infiltration rate (cm/min)	1.8±0.6	0.7±0.3	2.6±1.2	3.1±1.5	3.3±3.3	1.1±0.5
Soil pH	8.1±0.1	7.6±0.4	7.9±0.4	8.0±0.3	8.1±0.2	8.1±0.1
Salinity (ppm)	11,200±10,500	353±120	490±450	281±470	147±47	133±10
Biotic characteristics						
Living cover (percent)	12.0±6.8	14.6±4.0	19.4±6.4	27.0±6.5	26.2±6.8	21.8±4.2
Composition of cover (percent)						
shrubs	46±16	36±7	34±15	34±11	43±18	40±11
perennial forbs	2±3	14±5	6±4	16±8	11±4	20±11
perennial grasses	7±18	18±15	33±18	40±17	26±23	25±17
annuals	14±12	32±15	27±14	10±7	20±12	15±13
Species richness						
No. spp./0.25m^2	2.0±0.9	2.8±0.7	3.2±0.9	3.6±0.8	3.3±0.9	4.1±0.4
No. spp./0.05 ha	6.8±4.1	23.5±4.6	25.0±4.7	26.8±4.2	23.5±4.1	25.8±2.0

Table 2.--Average percent absolute frequency of the most abundant species in each of the six vegetative types recognized in this study. The frequency values of the 10 commonest species in each type are underlined. Each species is listed for all communities of occurrence. Frequency is the percentage of quadrats in a stand that contains the species in question

Species (life-form[1])	Mat saltbush	Green molly/ shadscale	Shadscale/ grass	Grassland/ shrubs	Blackbrush	Sagebrush
Androstephium breviflorum(F)	4	1	4	6		
Artemisia tridentata(S)						40
Aster arenosus(F)			2	9	5	15
Astragalus lentiginosus(F)		17		3	1	1
Atriplex confertifolia(S)		16	26	6	3	
Atriplex corrugata(S)	47			1		
Bouteloua gracilis(G)				6	9	15
Camissonia eastwoodiae(A)	23		1			
Chaenactis macrantha(A)		27				
Chaenactis stevioides(A)		1	14	4	15	16
Cleomella palmerana(A)	43					
Coleogyne ramosissima(S)				2	32	
Cymopterus purpurascens(F)		19	1	3		
Ephedra torreyana(S)			2	17	19	5
Eriogonum deflexum(A)			7	11	1	1
Eriogonum inflatum(A)	3	1	21			
Festuca octoflora(A)		9	16	14	18	27
Gilia leptomeria(A)	1		23	28	20	25
Gilia scopulorum(A)				8	40	57
Grayia spinosa(S)				4	12	3
Gutierrezia sarothrae(S)		1	12	34	11	51
Hilaria jamesii(G)	1	14	40	55	36	34
Kochia americana(S)		32		1		
Langloisia setosissima(A)		21	10	1		
Lappula occidentalis(A)		14	2	1		1
Lepidium montanum(F)			2	14	17	39
Mentzelia albicaulis(A)		1	6	24	25	14
Oryzopsis hymenoides(G)	11	21	17	25	9	25
Phacelia demissa(A)	40	15	20			
Salsola iberica(A)	22	6	23	9		
Sporobolus cryptandrus(G)			3	10		

[1]Letter following plant name indicates life form; S=shrub, G=perennial grass; F=perennial forb; A=annual.

ramosissima); and big sagebrush (Artemisia tridentata) (tables 1 and 2).

The distribution of vegetative types on the lower benchlands mirrors local parent materials (table 1). Exposures of Tropic shale support mat saltbush and widely spaced plants of Indian ricegrass (table 2). In years of above-average precipitation, adapted annual plants may flourish. In 1974, Cleomella palmerana, Phacelia demissa, and Camissonia eastwoodiae were abundant on sites derived from Tropic shale. Soils derived from Wahweap sandstone are dominated by shadscale and galleta grass on the lower benchlands and contain far less soluble salt and more sand than associated soils derived from Tropic shale. Although precipitation is probably comparable among the lower benchland study areas, the less saline, lighter-textured soils derived from the Wahweap sandstone supported about 60 percent more (in relative terms) plant cover than associated soils formed from Tropic shale. Floristic richness and vegetational composition also differ significantly on those two substrates with the former supporting a richer flora, relatively less shrub and annual plant cover, and relatively more perennial herb cover (table 1).

In areas where erosion has washed Tropic shale materials over rubble from Wahweap sandsone, green molly and shadscale grow intermixed with galleta, Indian ricegrass, and a variety of native annuals (tables 1 and 2). Surface soil characteristics at such sites are intermediate between those for exposures of Tropic shale and Wahweap sandstone in respect to texture, but such sites often have more stones in the profile than either of the other soils (table 1). Species richness (number of kinds of vascular species/quadrat or per stand) and vegetational composition on the alluvial soils that are derived from both Tropic shale and Wahweap sandstone are intermediate to values for those parameters on either of the parent materials alone (table 1).

On the upper benchlands, the three vegetational types sampled occurred on soils that were similar in respect to both textural and chemical characteristics (table 1). Nevertheless, soils underlying the grassland-shrub type were

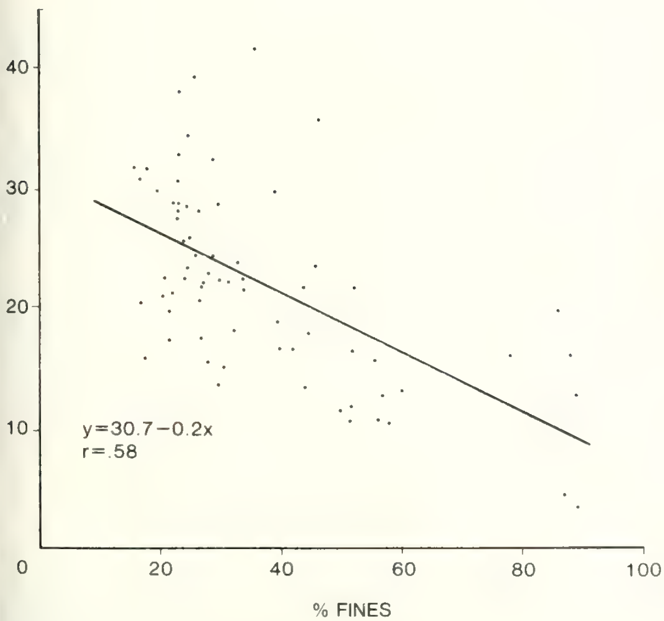
ignificantly deeper than those under either lackbrush or sagebrush stands. The latter two ommunity types characteristically appear on teeper ridges where natural erosion is slowly, ut steadily, removing surface material to djacent, less steep terrain. The rassland/shrub community often occurs on such ites where natural soil development is upplemented by light alluvial depositions from earby, low ridges. The grassland/shrub, lackbrush, and sagebrush communities are imilar in respect to total plant cover and ominant species, but the grassland/shrub type onsistently supports relatively more grass and ess shrub and annual plant cover than the two rush communities (tables 1 and 2).

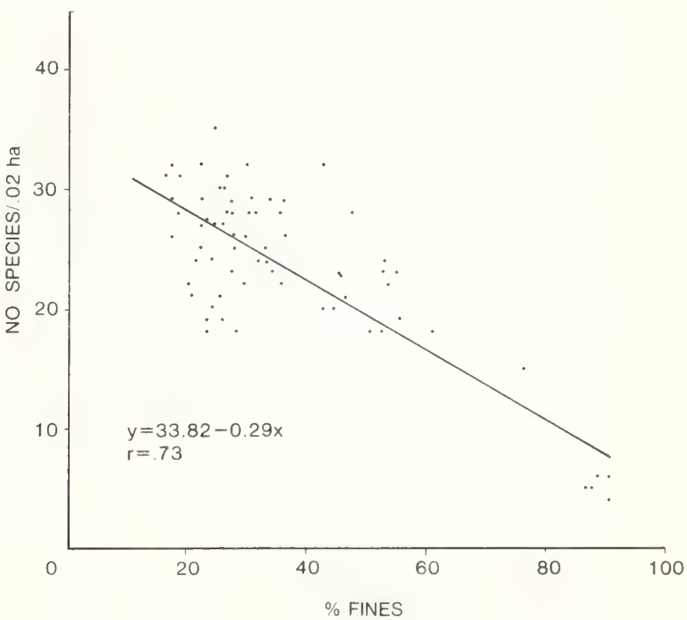
he blackbrush and sagebrush sites in our data et are essentially identical for soil texture nd soil depth, salinity, and pH (table 1). agebrush stands occur at slightly higher levations in the area, but the difference is ever large. The elevation difference should roduce slightly more precipitation and somewhat ooler temperatures at the sagebrush sites, but he difference does not seem large enough to liminate the possibility of blackbrush invading uch sites. It is known that sagebrush reinvades apidly after wildfire (Blaisdell and others 982), but blackbrush reinvades so slowly that ven after 35 years it may not be an important omponent of the vegetation (Callison and others 983). Fire scars in the woody vegetative types f the upper benchlands of our study area demonstrate that wildfires do sweep the area at least occasionally. We suggest that although there is a widespread tendency for blackbrush to dominate the shallowest, residual soils overlying coarse-textured rock in our study area, the current patterning of sagebrush and blackbrush on soils of intermediate or greater depth may be related to the history of local fires. Sagebrush may now occur on some sites that once supported blackbrush. The ability of sagebrush to reinvade after fire should give it an advantage over blackbrush on transitional sites where both species can survive.

Predictive Equations

When mine spoils are to be revegetated, it would obviously be helpful to know how much plant cover one might reasonably expect a particular combination of soil and topography to support in a given climatic zone. It, likewise, could be useful to know if species of a particular life-form class might be at an advantage on a particular site.

Our data demonstrate that soil texture is a strong variable that exerts a profound influence on both plant cover and species (fig. 2). Other single variables that significantly affected many biological parameters were elevation, slope position, and soil depth. Elevation probably exerts its effects through precipitation and ambient temperature; both would have a tendency to





igure 2.--Influence of soil fines (percent silt and clay summed) on living plant cover (left) and number f vascular species per 0.05-ac (0.02 ha) stand (right) at 72 stands on the Kaiparowits Plateau, Kane Co., T. Data collected in May 1975. Since precipitation for the period October 1, 1974 through May 21, 1975 as almost 46 percent (2.49 inch [6.1 cm]) above the long-term average and mean monthly temperature for hose months was 3.5 percent (ca. 1.48°F [0.7°C]) below long-term average, cover and species richness alues probably overestimate long-term averages for those parameters (U.S. Dept. Commerce 1974, 1975).

Table 3.--Multiple regression equations for various vegetational parameters. For these analyses, data from 72 stands in six vegetation types have been pooled. All equations are significant at the 0.01 level

Dependent variables	Regression equation	R^2
Total living cover	Y= 53.3 -0.22 Sa -0.33 Ro -0.54 Cl -0.0003 Sal	0.59
Shrub cover (percent total cover)	Y= -9.2 -4.44 SP -0.24 SD +0.29 Cl +0.92 %S +0.035 El	.33
Perennial forb cover (percent total cover)	Y= -20.3 +0.19 Ro -0.10 Cl -0.40 %S +0.024 El	.30
Perennial grass cover (percent total cover)	Y= 62.1 +8.64 SP +0.37 SD -0.71 Cl -0.78 S -0.027 El	.47
Annual cover (percent total cover)	Y= 50.6 -3.16 SP +0.51 Cl -0.024 El	.40
No. species per 0.25 m^2 quadrat	Y= 1.0 +0.16 SP +0.007 SD -0.03 Cl +0.002 El	.32

Key to symbols: Cl=percent clay, Sa=percent sand, El=elevation (m), Sal=salinity (ppm), Ro=percent rock, Percent S=percent slope, SP=slope position, SD=soil depth (cm) (See Methods for coding).

make more water available for plant growth as elevation increased. Others have elsewhere noted the effects of slope position on both living plant cover and composition (relative contribution of shrubs, grasses, forbs, and annuals) in local situations (Harner and Harper 1973; England 1979; Moretti and Brotherson 1982). Soil depth has an impact on both water and mineral resources available to roots at any particular point.

Multiple regression equations relating six dependent parameters (living cover, species per quadrat, and relative importance of shrub cover, perennial grasses or forbs, or annuals) to environmental variables at the 72 study sites are given in table 3. In all cases, the equations account for a highly significant amount of the variation in the dependent variables using five or fewer variables. Multiple correlation coefficients for the analyses ranged from a high of almost 0.77 for total cover to a low of 0.55 for forb cover.

The relative success of each of the four life-form groups (shrubs, perennial grasses, perennial forbs, and annuals) was dependent on a unique set of variables. Although percent clay in the soil was a component of each equation for life-form groups, it was positively correlated with annuals and shrubs, but was negatively correlated with relative success of perennial grasses and forbs. Elevation also appears in all four equations; but is positively correlated with shrub and forb success, but negatively associated with grasses and annuals. Slope position is a component of three of the equations (not significantly correlated with forbs). Slope position is negatively correlated with success of shrubs and annuals, but positively associated with an increasing grass component in the vegetation (table 3). Slope steepness was a component of three of the life-form group equations. The variable was positively correlated with shrubs and negatively related to success of both perennial grasses and forbs.

As we have shown elsewhere (Jaynes and Harper 1978), the major species of table 2 also respond strongly to the same variables shown to be significant for success of the various life-form groups here. Persons interested in predictive equations for performance of individual species should consult that paper.

The number of species encountered per quadrat was positively correlated with slope position (greatest at slope base), soil depth, and elevation; and negatively associated with increasing amounts of clay in the soil.

DISCUSSION

Vegetational patterns in the Kaiparowits Plateau region are primarily controlled by variation in soil parameters, especially within a given range of elevation. Where topography is relatively simple and elevational variation is moderate, as it was in this study, climatic and microclimatic parameters do not exert overwhelming impacts. Soil texture, slope position, and slope steepness were particularly potent variables. Their impact was probably expressed through soil moisture available for plant growth. Although increasing elevation is a nonclimatic variable, it appears to be a surrogate variable that has effects similar to decreasing temperature and increasing precipitation. In general, our multiple regression equations (table 3) suggest that available soil moisture is the most critical variable controlling both amount of plant growth and kinds of plants that can tolerate specific sites. Any of the many edaphic and topographic variables that affect soil moisture available to plant roots appear to be important to plants in the Kaiparowits region.

In this paper, we have not emphasized statistical analysis of individual plant species, since we chose to focus on regional patterns, and no plant species occurred in all six of the ecosystems considered. Our analyses suggest that species of similar life-form and/or longevity tended to respond somewhat similarly to the environmental complexes encountered in this study. Such a broad generalization will inevitably have many exceptions, but a variety of studies demonstrate that plants of similar life-form have much in common in respect to rooting depth (Stewart and others 1940), tissue

water content (Sharif and West 1968), phenology (Rabinowitz and others 1979; Kemp 1983), tissue chemical content (Harner and Harper 1973; Pederson and Harper 1979; Woodward and others 1984), and reproductive biology (Ostler and Harper 1978; Harper 1979). Those similarities were apparently sufficiently distinct among life-form groups that each group responded differently from all other groups (table 3) with many of the intergroup differences being statistically significant.

Assuming that our results for life-form group responses to environment are real and applicable in other deserts, managers concerned with revegetating disturbed lands can profitably use such relationships to determine a mix of life-forms most likely to succeed on a particular site. Once that decision is made, attention can be directed toward selection of well-adapted species in each life-form class. Such an approach seems more likely to result in successful, self-sustaining revegetation attempts than one in which species are selected without regard to life-form and predicted success of various life-forms on the site.

The soil and topographic variables considered in our study can be easily quantified at specific reclamation sites. When overburden materials are severely disturbed, growing conditions of resultant sites may be so different from those on nearby, undisturbed soils that little relevant information about suitable species for reclamation can be inferred from the natural plant cover. In such cases. equations such as those in table 3 (but derived from local samples) may provide useful guidelines for the kinds of species needed and the amount and composition of vegetation that can be expected when the reseeded cover finally comes to equilibrium with the local environment.

As Aldon (1984) has noted, "Mining reclamation specialists and government regulators need sound criteria for judging when reclamation is complete and expensive bonds can be released." The methods outlined here provide a realistic, manageable method for estimating how much plant cover a site can be expected to support. They also permit managers to predict the life-form spectrum that is "natural" for a specific site and a level of species richness (number of species per unit area) that approximates that of undisturbed sites having similar physical and chemical properties.

ACKNOWLEDGMENTS

Drs. J. R. Murdock, S. L. Welsh, and B. W. Wood provided technical and logistics support without which this project could not have been done. Holly Nichols, Steven Spencer, and Margaret Trimble assisted in all aspects of the study. The project was supported by NSF Grant EPP75-04397.

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COMPOSITIONAL PATTERNS WITHIN A RABBITBRUSH (CHRYSOTHAMNUS)

COMMUNITY OF THE IDAHO SNAKE RIVER PLAIN

Roger Rosentreter

BSTRACT: Species compositional patterns of an rea dominated by Chrysothamnus nauseous ssp. onsimilis and Poa sandbergii were investigated outh of Boise, ID. Two species associations, 1) rabbitbrush-Poa-moss and (2) lichen soil rusts, were identified. These associations orrelated with sites of contrasting soil epth, light intensities, and salt concentra-ions. Lichen soil crusts produce few ire-supporting fuels and may function as efugia. They appear to influence the post-ire composition of the entire study area.

NTRODUCTION

he ecology of plant communities can be viewed t various spatial scales, ranging from fine-rained patterns of competition or microclimate o global distribution patterns. Depending on he size of our observational window, different actors are important in controlling the istribution and abundance of plant species. his paper gives a descriptive account of the nterspecific relationships within a single lant community. The high diversity and bundance of soil cryptogams in this plant ommunity as well as the larger more obvious ascular plants, are described.

ften, the results of plant studies conducted ver the course of only 1 or 2 years merely eflect the weather conditions of those years ather than elucidating the long-term ontrolling biotic and abiotic factors. ryptogams such as lichens are long-lived, ersistent plants with slow growth rates. nlike any other plants, lichens are not reatly influenced by short-term weather onditions. This makes them ideal indicators f long-term climatic and environmental factors.

enerally lichens growing as thin crusts over oil are difficult to physically preserve ntact and as a result are poorly known axonomically. Ecological studies of plants re normally preceded by taxonomic studies, but his was not the case for this study in southwestern Idaho. In fact, only a few of the taxa in the study area were previously reported in Idaho (Schroeder and others 1975).

Cryptogamic soil crusts are common in seral rabbitbrush communities and continue to exist in the later successional Artemisia communities. Most of the cryptogamic lichen taxa in the study area have worldwide distribution and are reported from many other arid biomes (Rogers 1977). Arid-zone lichen floras from various continents are very similar, perhaps because of the wide ranging dispersal of their small fungal spores (Rogers 1977).

For example, Caloplaca tominii Savicz, characteristic of the Fulgensio-Calopacetum tominii synusia found within the Artemisia/ Agropyron community of the Canadian Yukon, was reported new to North American by Nimis (1981). Besides Caloplaca tominii, the Canadian Yukon plant community contains several lichen species that commonly occur in the southwestern Idaho study site. Caloplaca tominii also occurs in the Artemisia/grasslands of Russia (Savicz 1930) and northern Afghanistan (Poelt and Wirth 1968).

Studies of lichen communities that do not include associated vascular plant communities cannot produce correlating relationships or indicator values. Vascular plants and lichens read environmental factors differently and on separate time scales (McCune and Antos 1982). Each group of plants can provide information which may complement or explain something about the other. Descriptive studies such as this one are important for providing baseline data, identifying environmental indicators, and generating hypotheses. This study also attempts to evaluate the enhancement of vascular plants by cryptogams. In North America, there have been several phytosociological and floristic studies in arid habitats including those of Looman (1964a and 1964b), Anderson and others (1982), and Nash and Moser (1982).

STUDY AREA

The study area was located in Ada County south of Boise, ID. Elevation was 2,780 ft (848 m). The area is presently in a seral stage dominated by Chrysothamnus nauseosus ssp. consimilis and Poa sandbergii. Chrysothamnus nauseosus commonly resprouts after fires. Potential

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vegetation for the site is Artemisia tridentata ssp. wyomingensis/Agropyron spicatum habitat type (Hironaka and others 1983). This study area has an uncommonly high frequency of rabbitbrush, yet other nearby disturbed areas are dominated by cheatgrass and lack any shrub cover.

The soils in the study area were derived from basaltic parent material and loess over alluvial and lacustrine sediments. These soils fit the Chilcott and Sebree complex series which occur on nearly level or gently sloping positions (USDA 1980; Barker and others 1983). The Chilcott soil is a fine, montmorillonitic, mesic Abruptic Xerollic Durargid (USDA 1980). The Sebree soil is a fine-silty, mixed mesic Xerollic Nadurargid (USDA 1980). Mean annual precipitation is approximately 10 inches (25 cm). The site contained numerous randomly occurring natric, (slick) spots which contain shallow Sebree soils of poor drainage and a very low percentage of vascular plant cover. Natric spots are areas of high salt concentrations in the soil (Barker and others 1983).

The area has a history of environmental disruptions. Historically, it was impacted by travelers using the Oregon Trail (Yensen 1980), and presently it is grazed by sheep and cattle in both the spring and winter. Since the area is near Boise, ID, which is a large city, human disturbance includes assorted off road vehicle use, target shooting, rodent hunting, and bird watching. The Snake River Birds of Prey Natural Area is also nearby.

METHODS

Sampling Methods

Sampling took place in the spring. One hundred forty plots, 20 per transect line, were placed on seven different randomly distributed transect lines within the apparently homogenous Chrysothamnus nauseosus ssp. consimilis-Poa sandbergii community. Each transect line end point was marked with a permanent wooden stake and referenced by compass bearings. Plots were 7.9 X 19.7 inches square (2 X 5 dm) and were placed one meter apart along the transect lines. All species present were recorded by Daubenmire cover classes (Daubenmire and Daubenmire 1968). Soil depth to the duripan horizon and presence of vesicular porosity were recorded for each plot sampled. (Vesicular porosity is associated with low organic matter in the soil, USDA 1980).

Nomenclature of vascular plants, mosses, and lichens follows Hitchcock and Cronquist 1973, Conard 1956, and Hale and Culberson 1970, respectively. Taxonomic concepts for the lichen Aspicilia desertorum (Kremp.), Meresh. follow Weber (1962 and 1967) and the genus Psora follow that of Schneider (1979).

DATA ANALYSIS

Species Ordination

A polar ordination was used for the species ordination; it was prepared using the computer program SWAN (McCune unpublished). Several species were grouped for analysis due to difficulty in distinguishing them at the species level when sampling. Those species groups included: (1) Large mustards-Erysimum occidentale and Lepidium perfoliatum; (2) mosses other than Tortula which included Polychidium piliferium, Ceratodon purpureus, Bryum argenteum, Bryum spp., and Funaria hygromitrica; (3) Caloplaca spp. which included Caloplaca tominii, C. citrina, C. vitellina, and Candelariella terrigena; (4) Collema spp.--Collema tenax and Polychidium albociliatum. Other incidental species present but not treated in the ordination analysis follow:

VASCULAR PLANTS
Allium nevadense
Elymus cinerus
Microsteris gracilis
Ranunculus glaberrimus
Salsola kali
Sitanion hystrix

LICHENS
Acarospora schleicheri
Dermatocarpon cinereum
Diploshistes scruposus
Lecanora pergibbosa
Lecidea glaucophaea
Lecidea uliginosa
Massalongia carnosa
Parmelia elegantula
Peltigera rufescens
Physconia detersa
Psora cernata
Psora decipiens
Psora lurida
Psora luridella
Psorotichia nigra
Tonnia caeruleonigricans

LIVERWORTS
Clevea hyalina
Riccia beyrhichiana

FUNGI
Galerina spp.
Geastrum spp.
Ompholina ericetorum
Tulostroma spp.

Subjective end-stand selection ordinated the species in species space. This ordination was done on two axes. The first axis was between a natric indicator species, Lecanora muralis, and bare non-natric soil lacking vesicular porosity. The second axis was between a small shallow-rooted ephemeral species, Draba verna, and a larger diffuse deeper-rooted winter annual, Bromus tectorum. Species of this ordination were:

1. Chrysothamnus nauseosus ssp. consimilis
2. Chrysothamnus nauseosus (dead shrubs)
3. Poa sandbergii
4. Vulpia octoflora
5. Ranunculus testiculatus
6. Myosurus aristatus
7. Draba verna
8. Lithophragma bulbiferia
9. Large mustards
10. Bromus tectorum
11. Gayophytum ramosissimum
12. Tortula ruralis
13. Other mosses
14. Lecanora muralis
15. Caloplaca spp.
16. Lecidea sp. nov.
17. Dermatocarpon lachneum
18. Thrombium epigaeum
19. Arthonia glebosa
20. Collema spp.
21. Cladonia pyxidata
22. Aspicilia desertorum
23. Texosporium santi-jacobi
24. Bare non-natric soil

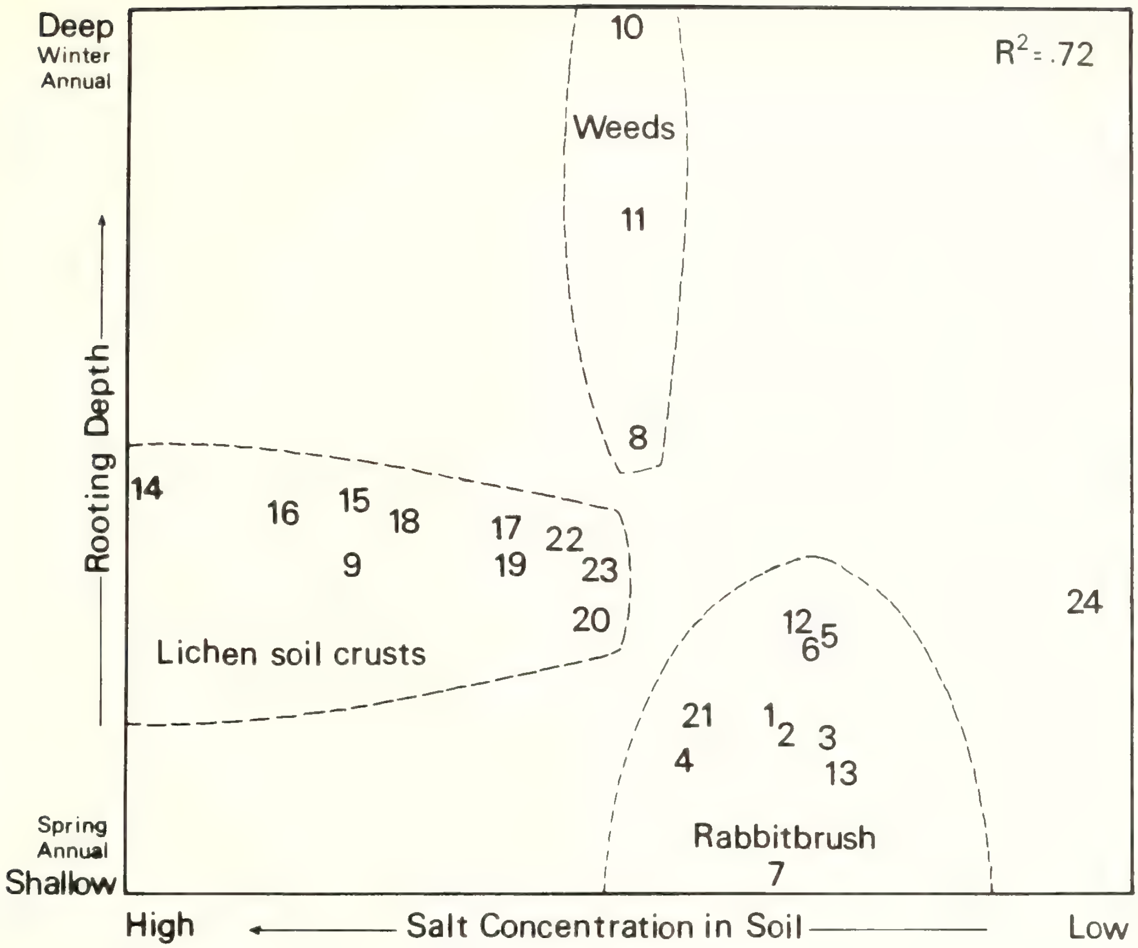

Figure 1.—Polar ordination of a rabbitbrush community.

RESULTS AND DISCUSSION

Discussions below are related to the ordination of species in Figure 1. The ordination of species suggests that the rabbitbrush community had two distinct species groups (1) the rabbitbrush-*Poa*-moss group and (2) the lichen soil crusts group. This ordination provides a helpful graphic representation of species similarity. This graphic presentation of the community structure allows for interpretation by both continuum and discrete ecological points of view. The other species cluster was composed of the weedy species. The weeds occurred centrally in the ordination showing that they have little site preference. In the field these weedy species obscured the pattern of the more site specific species.

Relationships Between Species Groups

The two species groups were predominantly separated by the first axis of the polar ordination (fig. 1). This axis was related to contrasting salt concentrations and resulting soil characteristics and represented a complex of factors associated with shallow natric soils. Shallow, natric or high sodium, soil sites accumulate silts and salts from local internal drainage. Sodium molecules bind the silt particles together, sealing the soil surface, preventing water penetration and creating standing water. These sites are called slick spots (USDA 1980). Water is lost by evaporation that concentrates the salts. Vascular plants' higher metabolic oxygen requirements preclude them from occupying such flooded anaeorobic sites. The shallow soil depth 1 to 4 inches (2 to 10 cm) and the duripan horizon restrict root penetration. Lichen soil crust species have low metabolic requirements making them tolerant of periodic flooding. Lichens lack roots and thus are not hindered by the shallow soil depth. Soil properties that characterize conditions of poor aeration appear to control the distribution of these species groups. This is similar to the reasons for the distribution pattern of big and low sagebrush, *Artemisia tridentata* and *A. arbuscula* (Hironaka and others 1983). These soil relationships point out that botany does not stop at the surface of the ground. The shallow natric soil sites lack shrubs and have little to no vascular plant cover. This results in little competition for light, moisture, nutrients, or space.

The second axis of the polar ordination was also related to soil depth. This axis appeared to separate vascular plant species which have roots and not the lichen species.

Relationships Within Species Groups

Rabbitbrush-Poa-moss.--The rabbitbrush-Poa-moss group occurred on the deeper non-natric soil, which was by far the more productive site. This rabbitbrush group contained only one lichen species, Cladonia pyxidata which occurs in many other more moist vegetation types. Cladonia pyxidata appears to be closely allied to this species group. All the moss species were closely associated with rabbitbrush, as was Poa sandbergii. One moss species, Polychidium piliferium, occurred on the dead portions of the short-lived perennial, Poa sandbergii clumps. In addition, seedlings of Poa sandbergii were most commonly found growing in beds of the moss Tortula ruralis. Several small shallow-rooted ephemeral annuals also occurred in these moss beds.

Lichen soil crusts.--The lichen soil crusts group was on the shallower, less productive, natric soil site. This group contained few vascular plants, only the large mustards Erysimum and Lepidium. These mustards are salt tolerant and mature in late spring and summer after the natric sites lose their standing water. This site lacked vascular plant cover sufficient to carry a fire.

One lichen, Texosporium santi-jacobi, a monotypic genus, is noteworthy for its uncommon ornamentation and large spore size (30 to 45u). It is one of the few narrow North American endemic lichens, it is a disjunct from the Mohave Desert of California. There is no apparent reason for this disjunct pattern. This is the only known population in Idaho despite intensive searching in southwestern Idaho.

The lichen species most narrowly defined spatially occurred close to Lecanora muralis. The narrowly defined (salt-tolerant) species were those lacking asexual fragmentation. In contrast, lichen species capable of asexual reproductive fragmentation were more broadly defined, such as, Arthonia glebosa, Caloplaca tominii, and Collema spp. These latter lichen species were more similar to the rabbitbrush species group and some could be considered weedy species. Rogers (1977) reported a similar species of Collema to be a pioneer species in arid Australia. Lichens which reproduce by fragmentation are often better indicators of environmental conditions because they lack sensitive "seedling" stages of growth. Seedlings often require very different conditions than do mature plants.

These natric sites produce few fire-supporting fuels and may function as fire refugia for those species occupying the site. Weedy lichen species surviving within the natric sites then may reinvade the burned rabbitbrush-Poa-moss sites. The study area's species richness and abundant lichen cover may characterize this mottled pattern of natric sites as refugia from fire. The refugia provide the plants necessary for rapid reinvasion. Refuge sites also may provide firebreaks and cool spots in fires which promotes the resprouting of rabbitbrush. Supporting this concept is the fact that large Lecanora muralis individuals on the natric sites were estimated to be over 60 years old (annual increment 2 to 3 mm) (Hale 1974), yet the area burned only 17 years ago (BLM fire records).

This fire refugia concept suggests that the compositional pattern of species is fire dependent. Therefore, the presence of refugia sites appears to influence the postfire species composition of the entire study area.

Grazing by sheep and cattle may also affect the relationships among species groups. The lack of vascular plants on the open natric sites may be the result of livestock use of the easier accessed open areas. Also, compaction and trampling by livestock may encourage the crustose growth form of lichens. The study site does have a heavy cover of cryptogams. In contrast, Rogers and Lange (1971, 1972), Rogers (1974), and Anderson and others (1982) report less lichen cover on heavily grazed areas. The heavy lichen cover on this site may reflect the importance of natric spots in promoting lichen growth. It appears that dispersal sites are more important than the grazing pressure on the influence of lichen cover in this sagebrush/grassland habitat type. The natric sites also had heavier textured silty soils which have been reported to be favorable for lichen cover (Anderson and others 1982).

CONCLUSIONS

The lichen soil crusts group is apparently a climax edaphic group. If plant succession were allowed to occur without major disturbances, the rabbitbrush-Poa-moss species composition would change while the lichen soil crusts group would not.

Rabbitbrush stands appear to be favorable for lichen growth because they lack leaves in the winter and early spring; this allows penetration of sunlight to the soil surface. Rabbitbrush stands also collect blowing snow, and increase soil surface temperatures and humidity on sunny winter days.

This community was composed of a rabbitbrush-Poa-moss species group and a lichen soil crust group. The species composition pattern of this rabbitbrush community appears to be determined by fire and edaphic conditions. The edaphic pattern contained slick spots which act as fire refugia for lichen species. These slick spots also influence fire behavior, resulting in cooler fires which promote rabbitbrush resprouting. Thus, slick spots influence species composition on both slick and nonslick spots. In contrast, areas nearby which lack slick spots burn hotter and are dominated by cheatgrass.

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POPULATION DYNAMICS OF TWO SAGEBRUSH SPECIES AND

RUBBER RABBITBRUSH OVER 22 YEARS OF GRAZING USE BY THREE ANIMAL CLASSES

Richard Stevens

ABSTRACT: Density and growth performance of basin big sagebrush, white rubber rabbitbrush, and black sagebrush plants associated with grazing (blacktail jackrabbits, mule deer, and cattle) located in a fourway exclosure were identified and measured 2 (1964), 11 (1973), and 22 (1984) years following chaining and seeding of a juniper-pinyon site in central Utah. Considerable reproduction came from seed produced by native shrubs. Many shrubs were not killed by chaining. With no grazing, rabbit use only, deer use only, and rabbit and deer use combined, total numbers of big sagebrush and rabbitbrush plants decreased substantially between 1973 and 1984. With rabbit, deer, and cattle use combined these two shrubs and black sagebrush increased steadily.

INTRODUCTION

A majority of the winter and spring livestock and big game ranges in the Great Basin are located in the juniper-pinyon and sagebrush types (Ruess and Blanch 1951; Plummer and others 1970; Dwyer 1975). During the past three to four decades many of these rangelands have been treated mechanically or chemically and seeded (Plummer and others 1968; Vallentine 1971; Jordan 1982). Seed mixtures have included various grasses, forbs, and shrubs (Stevens 1983). Depending on site characteristics, species seeded and site preparation and seeding techniques, establishment of seeded species has been quite variable (Plummer and others 1970a, 1970b; Stevens and others 1977; Keller 1978; Jordan 1983), with shrub establishment being the most erratic. Reproduction of on-site species has been influenced by the density, condition, and age of the plants left on the site following treatment.

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Establishment success from direct seeding of basin big sagebrush (Artemisia tridentata ssp. tridentata), black sagebrush (A. nova), and white rubber rabbitbrush (Chrysothamnus nauseosus ssp. albicaulis) has ranged from poor to excellent (Van Epps and McKell 1980; Crofts and Carlson 1982; Colbert and Colbert 1983; Luke and Monsen 1984; Monsen and Richardson 1984). These three shrubs establish not only from artificial seeding, but by natural spread from remnant plants (Daubenmire 1975; Young and Evans 1978; Monsen and Richardson 1983; Young and others 1984).

The inclusion of sagebrush and rabbitbrush seed in a herbaceous seeding can increase total production, enhance grass yields (Plummer 1959; Frischknecht 1963), improve the nutritive value of the seeding (Welch 1983), increase available winter forage, enhance snow entrapment, improve the esthetics of the seeding, and reduce the chances of destructive insect infestations (Haws 1978).

This study was designed to gain a better understanding of how basin big sagebrush, black sagebrush, and white rubber rabbitbrush respond to removal of competitive vegetation, direct seeding, natural invasion, and grazing by deer, rabbits, and cattle.

AREA

The Fountain Green Wildlife Management Area is located 5 miles (8 km) northeast of Fountain Green, Sanpete County, UT. A portion of the area was chained and seeded with a mixture of grasses, forbs, and shrubs in the fall of 1962. White rubber rabbitbrush seed collected from Wales Canyon, 18 miles (29 km) southeast of the site and seed of basin big sagebrush collected on the site were included in the seed mixture. Black sagebrush was not seeded. Prior to treatment, the site supported juniper-pinyon (Juniperus osteosperma-Pinus edulis) with a fairly good understory of basin big sagebrush and lesser amounts of Indian ricegrass (Oryzopsis hymenoides), western wheatgrass (Agropyron smithii), black sagebrush, and white rubber rabbitbrush.

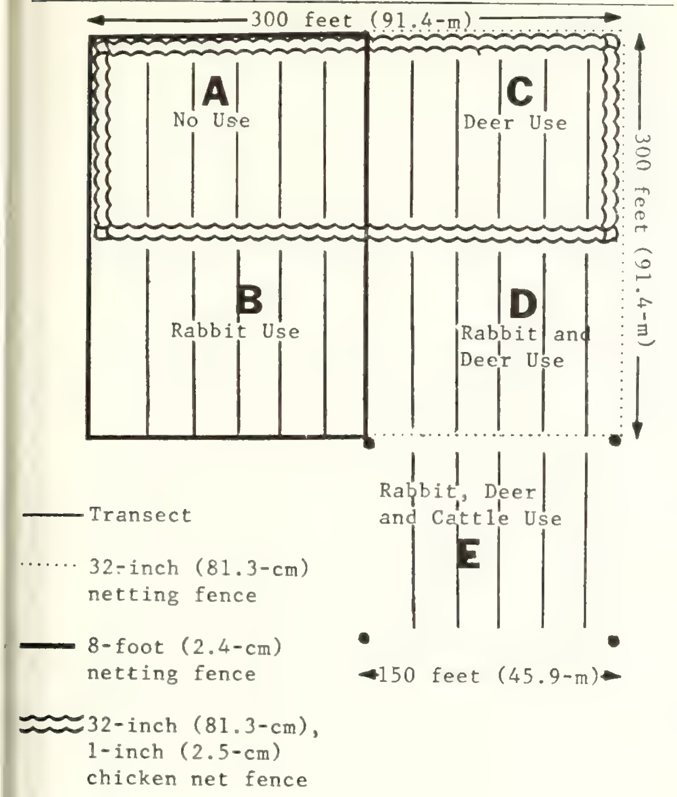

Figure 1.--Fountain Green fourway exclosure and comparable outside area. Five grazing treatments.

Following seeding a 300- by 300-foot (91.4- by 91.4-m) fourway exclosure (fig. 1) was built. The exclosure is located on a southeast exposure with an 8 percent slope. Soil is described as Deer Creek stoney silt loam (USDA 1981). Average annual precipitation during the 22-year study period was 14.73 inches (37.4 cm), with a high of 24.57 inches (62.4 cm) in 1983 and a low of 6.67 inches (16.9 cm) in 1976. The exclosure consisted of four 150- by 150-foot (45.7- by 45.7-m) sections. One section was open only to mule deer (Odocoileus hemionus) (treatment C), one to blacktail jackrabbits (Lepus californicus) (treatment B), one to both deer and rabbits (treatment D), and another closed to these animals and cattle (treatment A). An outside area of comparable size was open to deer, rabbits, and cattle (treatment E). Rabbit populations were high, being near or at peak the first 4 years following seeding. Mule deer numbers were moderate and remained fairly constant. Spring (May-June) use by cattle started 4 years after seeding and continued annually through 1981.

METHODS

Within each of the five sections, five permanent 100- by 1-foot (30.5- by 0.3-m) belt transects were randomly established to measure herbaceous growth and ground cover (fig. 1).

Percent cover of all herbaceous and woody species and production of herbs were recorded in 1964, 1965, 1967, 1972, 1977, and 1982. Ground cover was determined using a point sampling technique. A point was dropped at 6-inch (15.4-cm) intervals along each 100-foot (30.5-m) line (1,000 points per grazing treatment) with the first item encountered being recorded.

Cover data for 1964, 1972, and 1982 will be used as these 3 years corresponded the closest to the years that all shrubs were mapped and measured.

All shrubs and trees were mapped and their locations, widths, heights, and age classes recorded in all five grazing treatments in 1964, 1973, and 1984 (fig. 2). The following classes were applied. Basin big sagebrush and white rubber rabbitbrush height and age classes were: 0-5 inches (0-12.7-cm) (seedlings and young plants), 5-20 inches (12.7-50.8-cm) (immature plants), and over 20 inches (50.8-cm) (mature plants, producing seed). Black sagebrush classes were: 0-3 inches (0-7.6-cm) (seedlings and young plants), 3-10 inches (7.6-25.4-cm) (immature plants), and over 10 inches (25.4-cm) (mature plants).

Cover data are presented as trends. Shrub numbers are the total population of each species.

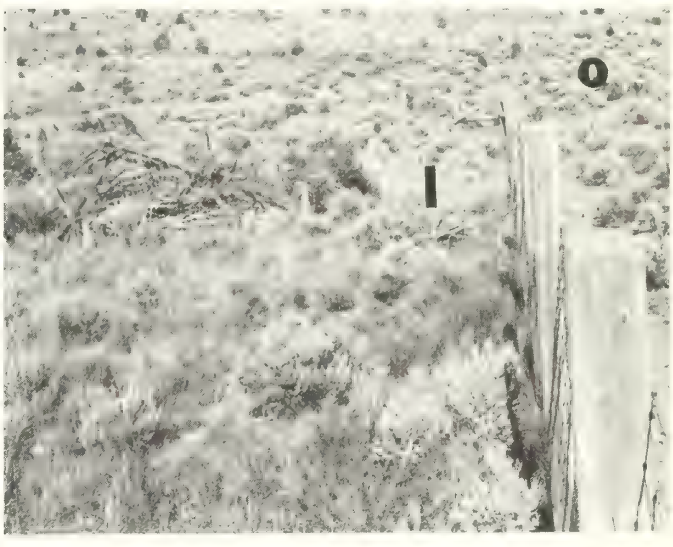

Figure 2.--Fountain Green exclosure, 1976. Total protection (treatment A, no grazing) section (I) and comparable outside (O) area (rabbit, deer, and cattle use). Note difference in shrub densities between sections and absence of forbs (alfalfa and Utah sweetvetch) in outside area.

RESULTS

Direct Seeding

The number of basin big sagebrush and white rubber rabbitbrush plants that resulted from direct seeding is unknown. The majority of the reproduction may or may not have originated from residual plants. The area was seeded in 1962; 2 years (1964) later shrubs were counted and measured. There were 52 basin big sagebrush; 1 seedling, 48 immature, and 3 mature plants. Nine white rubber rabbitbrush plants were immature; 1 was mature. Only one black sagebrush plant (mature) was located. Increase in shrub numbers after 1964 resulted from seed production off residual plants.

Cover, Production, and Numbers

Data indicate that total grass and forb production is more a factor of annual precipitation than it is of grazing treatments.

Percent cover appears to be a reliable indicator of community changes influenced by grazing treatments. Daubenmire (1968) reports similar results. Increases in shrub cover in all grazing treatments (fig. 2) corresponded with increased number of shrubs (fig. 3) and increased shrub size (figs. 4, 5, 6, 7, 8, and 9). The greatest increase in shrub cover (17 percent) was associated with the greatest increase in shrub numbers, and the largest number of mature shrubs. The greatest increases occurred where cattle, deer, and rabbits grazed jointly (treatment E).

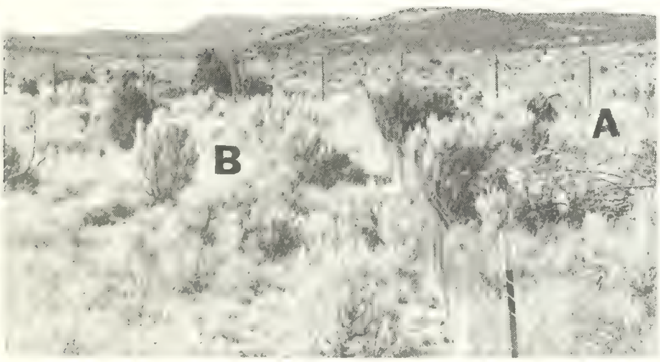

Figure 3.--Fountain Green Exclosure, 1976. Total protection from grazing (treatment A) (right) and rabbit use (treatment B) sections (left).

Forbs and grasses.--In 1964, 2 years following chaining, forbs attained their greatest amount of cover (13-29 percent) (fig. 4). The majority of the forbs were weedy annuals. On most juniper-pinyon improvement projects, annual forbs normally increase dramatically immediately following chaining. Once the seeded perennials became established, annual forbs decreased in number and cover until in 1972, when annuals made up less than 0.5 percent of the total cover. The seeded perennials, alfalfa (Medicago sativa var. Ladak), small burnet (Sanguisorba minor), and Utah sweetvetch (Hedysarum boreale) by 1972 had become firmly established and accounted for the majority of the forb cover. Under total protection from grazing (fig. 4, treatment A), perennial forb cover increased between 1964 and 1982. By 1982, forb cover under total protection was much higher (16.8 percent) than where rabbit (2.5 percent), or deer (6.2 percent), or rabbit and deer (3.8 percent) use occurred (treatments B, C, and D). Forb cover under cattle, deer, and rabbit use together (treatment E) steadily decreased from 18.2 to 1.9 percent.

Bare ground (fig. 4) steadily decreased (24.5 to 6.9 percent) where no grazing occurred (treatment A); however, there was an increase (16 to 25 percent) in bare ground where cattle, deer, and rabbits grazed together (treatment E). The increase in bare ground corresponds with: (1) increases in shrub numbers, and (2) decreases in forb cover. Litter (25 percent) and rock (5 percent) cover changed little over the study period.

Cover (25 to 35 percent) by grasses remained fairly stable over the years of the study and between grazing treatments. The first 2 to 3 years following chaining and seeding, the native grasses (Indian ricegrass and western wheatgrass) made up over 50 percent of the grass cover. As the seeded species established, they slowly became dominant. In 1982, native grasses under cattle, deer, and rabbit use did, however, maintain themselves as an important community component (over 30 percent). There were fewer trees alive in 1982 than in 1964; however, those alive had increased in size.

Basin big sagebrush.--Total number of shrubs appear to have been affected by grazing treatments (fig. 6). Within each of four grazing treatments; A. total protection; B, rabbit use; C, deer use; and D, rabbit and deer use combined, the total number of shrubs and the number of immature shrubs increased dramatically between 1964 and 1973 (A, 8 to 426; B, 15 to 558; C, 7 to 358; D, 3 to 453) and then decreased substantially between 1973 and 1984 (A- 426-333; B- 558 to 401; C- 358 to 173; D- 453 to 274). Only with combined rabbit, deer, and cattle use did number of shrubs increase from 1964 to 1973 (19 to 233) and again between 1973 and 1984 (233 to 465). Number of mature plants, however, increased during each time period in all grazing treatments.

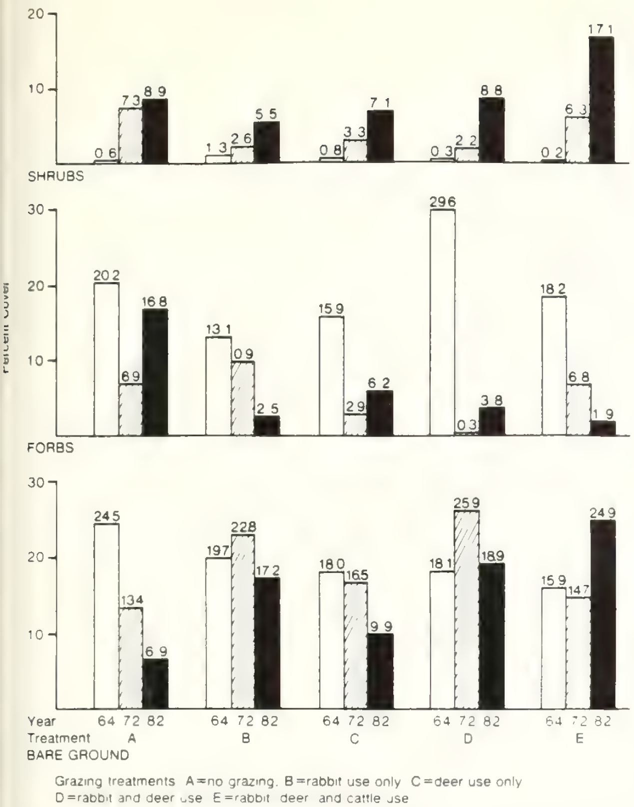

Figure 4.--Percent bare ground and percent ground cover of forbs and shrubs in 1964, 1972, and 1982, Fountain Green exclosures, five grazing treatments.

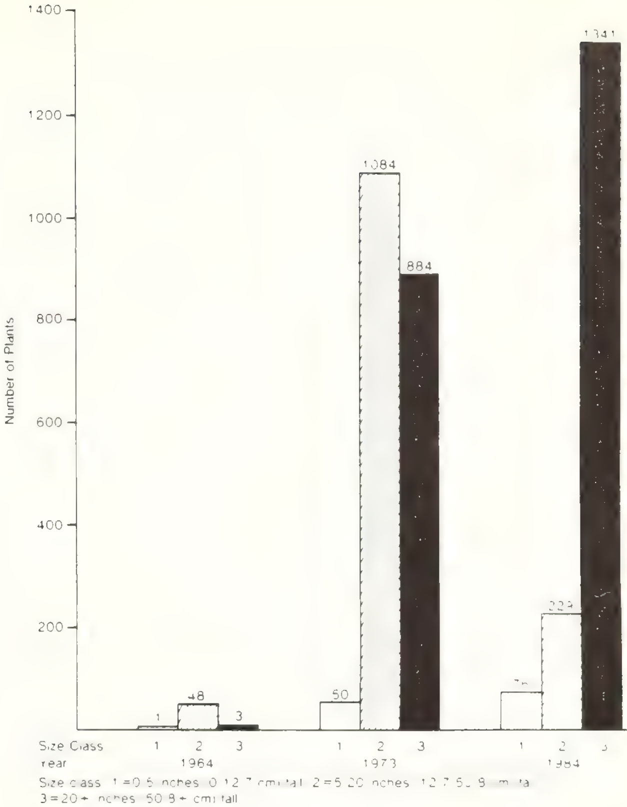

Figure 5.--Total number of basin big sagebrush plants (three size classes) in 1964, 1973, and 1984, Fountain Green exclosure.

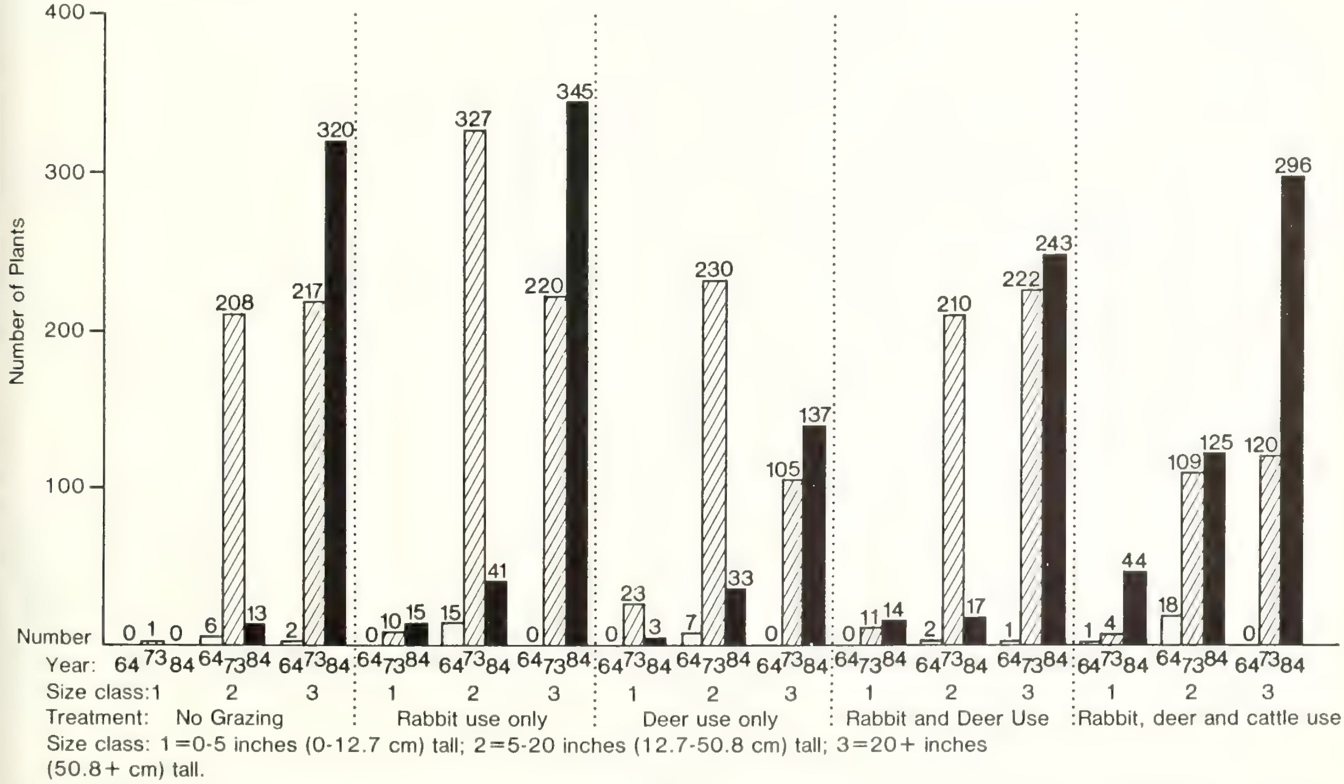

Figure 6.--Total number of basin big sagebrush plants (3 size classes) in 5 grazing treatments, Fountain Green exclosure, 1964, 1973, and 1984.

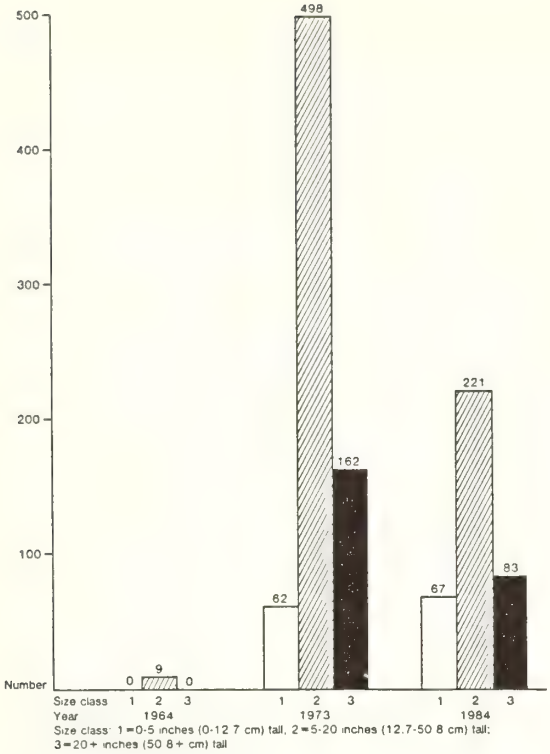

Figure 7.--Total number of white rubber rabbitbrush plants (three size classes) in 1964, 1973, and 1984, Fountain Green exclosure.

Fifty-two big sagebrush plants were present within the five grazing treatments in 1964. By 1973 there were 2,018 and in 1984 there were 1,646. Of the 52 original plants, 42 were alive in 1973 and 29 in 1984. About one-half (1,084) (fig. 5) of the 2,018 plants recorded in 1973 were immature; only 884 were mature. In 1984 there were 229 immature and 1,341 mature plants. Total number of plants increased dramatically between 1964 and 1973 followed by a substantial decrease between 1973 and 1984. Seedling numbers, however, showed a steady increase: 1 in 1964, 50 in 1973, and 76 in 1984.

White rubber rabbitbrush.--There were only 10 (9 immature, 1 mature) rabbitbrush plants in all grazing treatments in 1964. A dramatic increase to 622 plants occurred by natural spread between 1964 and 1973, followed by a nearly 40 percent decrease in numbers between 1973 and 1984 to 371 shrubs (fig. 7). Death of immature and mature plants between 1973 and 1984 accounted for the decrease. Number of seedlings was constant: 62 in 1973 and 67 in 1984.

There was at least a 65 percent reduction in the total number of rabbitbrush plants in four of the grazing treatments (total protection, rabbit, deer, and combined rabbit and deer use) (fig. 8) between 1973 and 1984. However, with combined rabbit, deer, and cattle use, rabbitbrush numbers increased from 47 to 239 during the same period.

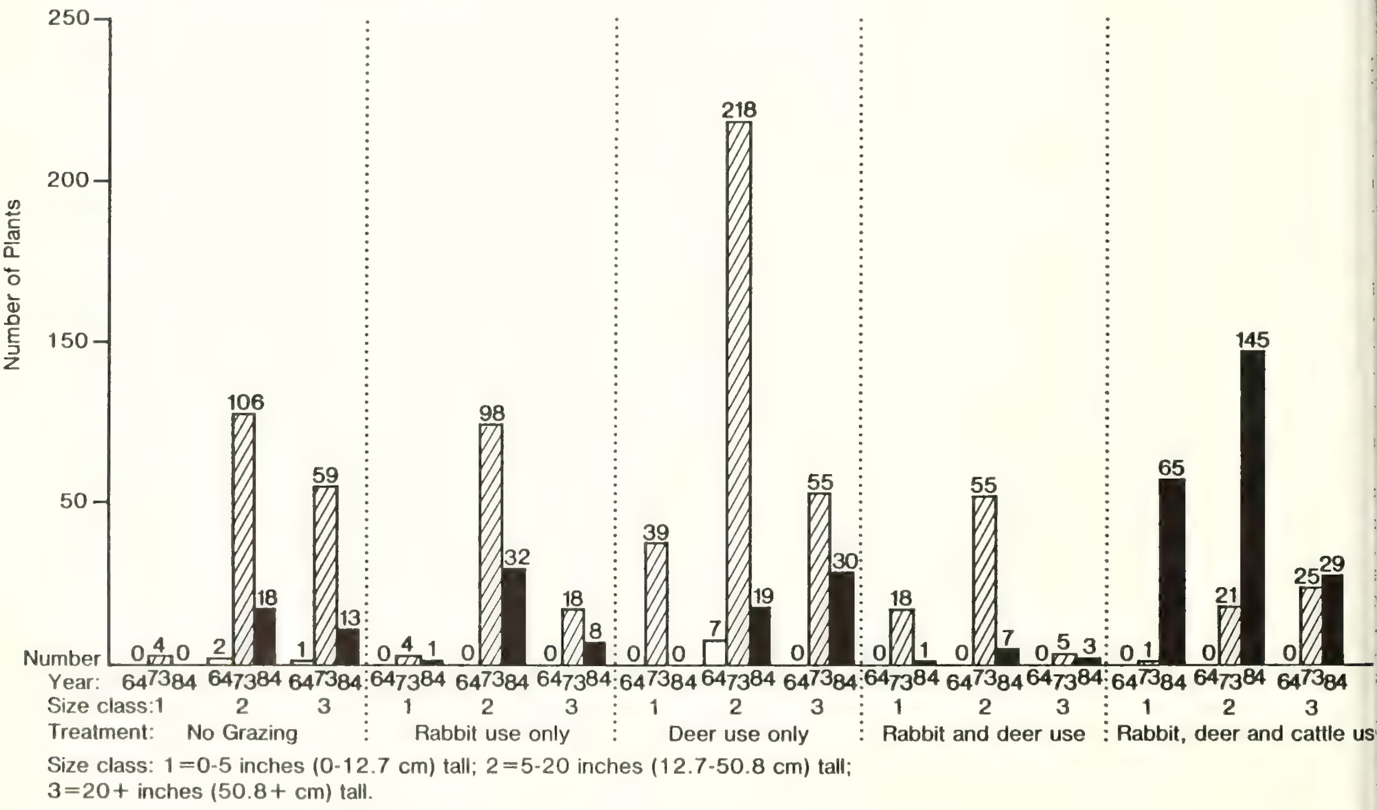

Figure 8.--Total number of white rubber rabbitbrush plants (3 size classes) in 5 grazing treatments, Fountain Green exclosure, 1964, 1973, and 1984.

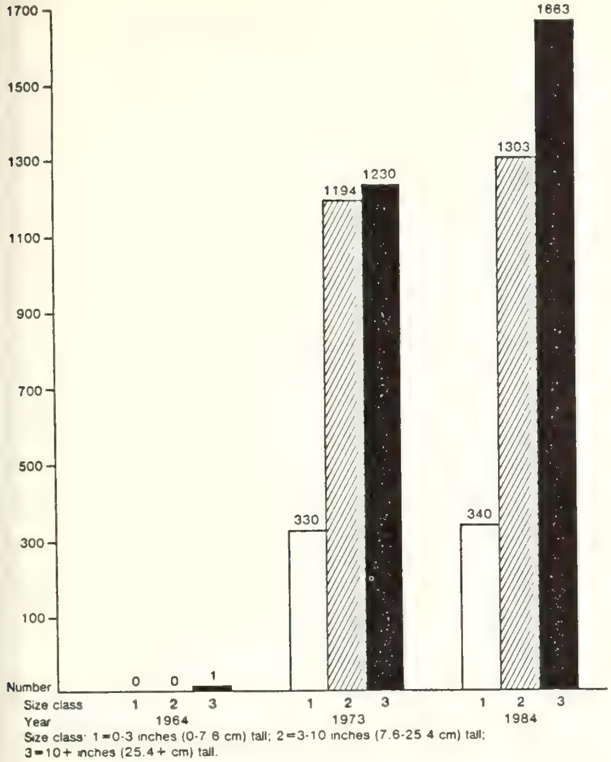

Figure 9.--Total number of black sagebrush plants (three size classes) in 1964, 1973, and 1984, Fountain Green exclosure.

Black sagebrush.--Within all five grazing treatments, shrub numbers were similar. Grazing treatment effects on shrub numbers were not evident. There was however, a dramatic change in total number of plants in all treatments over 22 years. One black sagebrush plant (mature) was located in 1964, 2,754 in 1973, and 3,306 in 1984.

Numbers of seedlings (fig. 9) in 1973 and 1984 were constant. Increases occurred in numbers of immature (1,194 to 1,303) and mature (1,230 to 1,663) plants.

SUMMARY

Fountain Green Wildlife Management Area was chained and seeded to a mixture of grasses, forbs, and shrubs in 1962. Basin big sagebrush and white rubber rabbitbrush were included in the seed mixture. Black sagebrush was not seeded. Chaining did not kill all the shrubs within the study area. All shrubs associated with a 300- by 300-foot (91.4- by 91.4-m) exclosure on the area were located and mapped in 1964, 1973, and 1984. Because of the short viability period of big sagebrush and rubber rabbitbrush seed (Stevens and others 1981; Jorgensen n.d.), only those shrubs on the sites in 1964 could have originated from seed planted in 1962. Goodwin (1956) reports that big sagebrush seed can move in the direction of prevailing winds up to 108 feet (33 m). Frischknecht (1962) followed big sagebrush reproduction in a crested wheatgrass (A. cristatum) seeding and reported that the maximum distance progeny spread from parent plants was 42 feet (12.6 m). Our observations are in line with these literature reports.

Numerically, black sagebrush increased the most of any shrub and did not appear to be affected by the presence or absence of grazing. Where rabbits, deer, and cattle grazed jointly for 22 years, big sagebrush and rubber rabbitbrush numbers showed the greatest sustained increase. This was the only grazing treatment that: (1) had a substantial increase in bare ground; (2) had the least amount of introduced perennial grasses; (3) had the lowest density of seeded perennial forbs (fig. 2); and (4) had the greatest amount of soil disturbance from grazing animals.

Big sagebrush, rubber rabbitbrush, and black sagebrush have been recognized as invader species (Frischknecht 1963; Christensen 1963), especially where the perennial grass community has been weakened. Vallentine (1979) also reported that continual early spring grazing encouraged invasion of big sagebrush. Continued early spring grazing by cattle occurred in the study area for 13 years; this may account for the continual increase in big sagebrush, black sagebrush, and white rubber rabbitbrush, along with an associated increase in bare ground and decrease in forbs and introduced grass cover (fig. 2).

Increased shrub numbers did not appear to adversely affect grass and forb forage production where no grazing occurred, or where rabbit use, deer use, and rabbit and deer use combined took place.

Basin big sagebrush, black sagebrush, and white rubber rabbitbrush were easily established, from direct seeding or residual plants in established stands of introduced and native perennial grasses and forbs.

ACKNOWLEDGMENT

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INFILTRATION ON OREGON LANDS OCCUPIED BY THREE SUBSPECIES OF BIG SAGEBRUSH

Sherman R. Swanson and John C. Buckhouse

ABSTRACT: High-intensity, short-duration rainfall events were simulated in the shrub interspaces on sites populated by three subspecies of big sagebrush, Artemisia tridentata ssp. tridentata, wyomingensis, and vaseyana, at four locations in eastern Oregon. Statistical analysis of infiltration during the final 15 minutes of each run showed large variability. Infiltration decreased as soil particle size decreased, organic ground cover decreased, bulk density increased, and extractable sodium increased. Infiltration was significantly lower on soils with vesicular porosity in the surface.

INTRODUCTION

Infiltration is necessary for precipitation to become part of the soil moisture available for plant growth. Infiltration of precipitation during the growing season can be especially important to herbaceous plant growth. Vegetation can in turn be influential in promoting infiltration, especially when percolation dominates the process.

The concept of using habitat types as a classification tool on western watersheds was promoted by Buckhouse and Mattison (1980) and Pfister (1981). The success of this concept depends on how well plant communities reflect watershed characteristics such as ground cover, above and below ground plant structure and phytomass, and soil structure, depth, texture, and organic matter.

Tisdale and Hironaka (1981) stressed the value of Artemisia tridentata (big sagebrush) subspecies in synecology. Winward (1980) briefly described management implications for A. tridentata subspecies.

Wyoming big sagebrush, A. tridentata ssp. wyomingensis, dominates the most xeric habitats of big sagebrush subspecies. It generally occurs below 6,000 feet (1 800 m) on moderately deep, well-drained soils. Grasses form the majority of the understory vegetation and most forbs are annual. There is a considerable amount of bare ground which cryptogams may occupy, 5 to 25 percent even under pristine conditions.

Basin big sagebrush, A. tridentata ssp. tridentata, occupies deep, well-drained soils and much of its range has been converted to cropland. More perennial forbs grow in these stands. Herbaceous production is from 1-1/3 to 2 times greater than in A. tridentata ssp. wyomingensis stands.

Mountain big sagebrush, A. tridentata ssp. vaseyana (var. pauciflorus) (Goodrich and others 1985), resides in the upper foothill and mountain areas from 3,500 ft (1 100 m) to 9,000 ft (2 700 m) elevation. It occupies moderately deep, well-drained soils with moisture available most of the summer. The herbaceous layer is more diverse, with commonly three to four times more species, and more productive by 1-1/2 to 2 times than on A. tridentata ssp. wyomingensis sites.

Our objectives were twofold: (1) Look for characteristic differences in infiltration rates among sites occupied by the three subspecies; and (2) identify aspects of the soil and vegetation that control and/or indicate differences in infiltration rates.

STUDY AREA AND METHODS

At each of four widely spaced eastern Oregon locations, (fig. 1) Millican, Squaw Butte, Frenchglen, and Baker, three sites for each of the three subspecies were selected; a total of 36 sites. Each site was relatively homogeneous and representative of a common habitat type in relatively high ecological status. The vegetation on most sites was classified as mid-seral or high seral. However, all but one of the A. tridentata ssp. tridentata sites were classified as low seral, often because of Bromus tectorum (cheatgrass) abundance. In general, A. tridentata ssp. vaseyana sites were in the best condition. To facilitate use of the Rocky Mountain infiltrometer (Dortignac 1951), each site was selected for nearness to a road, slight slope, and scarcity of large rocks that would interfere with placement of subplot frames.

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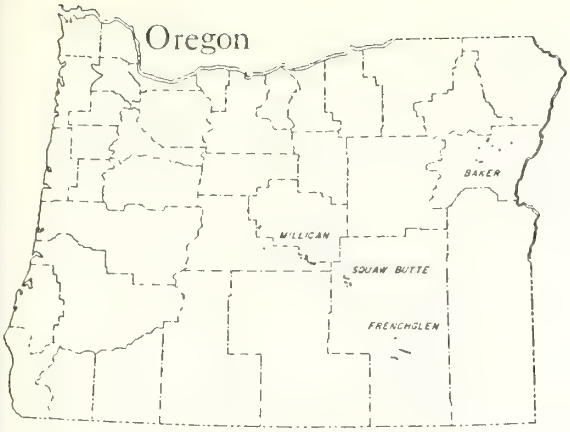

'igure 1.--Location of study sites.

'egetation and soils were described in 1980. 'egetation was surveyed with three frequency :ransects of ten 1- by 2-foot (30- by 61-cm) ılots each (Pieper 1978). Soils were described, ;ampled, and classified at the family level ıccording to standard Soil Conservation Service USDA Soil Conservation Service 1975) lefinitions.

ıll A. tridentata ssp. wyomingensis sites except me were Aridisols, whereas all A. tridentata ssp. 'aseyana sites were Mollisols. The A. tridentata ;sp. tridentata sites were about evenly divided ›etween these soil orders. Five of the Millican ;ites have been heavily influenced by surficial leposits of Newberry Crater or Mazama pumice tephra).

ıll twelve A. tridentata ssp. vaseyana sites and ıalf the A. tridentata ssp. wyomingensis had 'estuca idahoensis (Idaho fescue) as the ınderstory dominant (Doescher 1982). Three of the :emaining A. tridentata ssp. wyomingensis sites 'ere A. tridentata ssp. wyomingensis/Stipa :hurberiana (Thurber's needlegrass) habitat type; :wo were A. tridentata ssp. wyomingensis/Poa ;andbergii (Sandberg's bluegrass) habitat type; ınd one was A. tridentata ssp. wyomingensis/Stipa :omata (needle-and-thread grass) habitat type (Hironaka and Fosberg 1979). Half of the A. .ridentata ssp. tridentata sites were A. :ridentata ssp. tridentata/Elymus cinereus (basin 'ild rye) habitat type (Hironaka 1979); three were ı. tridentata ssp. tridentata/Agropyron spicatum (bluebunch wheatgrass) habitat type; and one was ı. tridentata ssp. tridentata/Stipa comata habitat :ype (Hironaka and Fosberg 1979).

'he following summer (1981) a Rocky Mountain :nfiltrometer (Dortignac 1951) was used on each ;ite to simulate high-intensity rainfall and ıeasure infiltration and soil erosion in shrub :nterspaces. The 5 inches/h (12.6 cm/h) simulated ;torms represented events with a return period of 'ell in excess of 100 years (Miller and others .973). At least 30 minutes before each run, ;ubplots were prewet with a fine-spray watering :an until ponding began. (Ponding was possible ›n one tephra-dominated site which produced no :unoff.) Each run lasted 28 minutes with samples collected after 3 minutes and at subsequent 5-minute intervals.

Eighteen subplots grouped into six plots were placed in representative shrub interspaces on each site. At each subplot, slope was measured with an Abney level and percentage coverage of each soil surface morphology type was visually estimated along with surface pavement, litter, cryptogams, bunchgrass base, and canopy cover. Litter and bunchgrass were combined to form the term organic ground cover. Training for ocular estimation of cover was done in the field with a 100-point frame.

Samples of the top 2.4 to 3.9 inches (6 to 10 cm) of each major soil surface morphology type were collected from two locations on the site to determine stone-free bulk density (Blake 1965), organic matter (Walkley and Black 1934), percentage medium and coarse sand, fine sand, silt, and clay in the fine-earth fraction (Day 1965), and extractable sodium (Peech and others 1947).

The three sites of each subspecies at each location served as replications for a randomized complete block experimental design with locations as the blocking factor and subspecies as the treatment. Simple and stepwise multiple correlation and one-way analysis of variance used sites or, where appropriate, plots or subplots as replications. Tukey's procedure was used for multiple comparisons of equal sample size and Scheffe's test was used with unequal sample size. Significance tests were made at the 0.1 probability level (Steel and Torrie 1980).

RESULTS

Average infiltration curves for the 36 sites were highly variable. Some sites showed almost no reduction in infiltration rate during the 28-minute run, while others showed rapid reduction in water intake before infiltration stabilized. Analysis focused on the last 15 minutes of the run (average final infiltration rate). Average final infiltration rates varied from just over 1 to just under 5 inches per hour (<3 - >12 cm/h). Habitat type and climax understory species showed no significant correlation with final infiltration rates. Although mean infiltration rates appeared generally lower for sites occupied by A. tridentata ssp. wyomingensis and for sites at Squaw Butte, statistical differences were not confirmed due to a significantly inconsistent variation between subspecies at the four locations (fig. 2). Differences in infiltration rates between sites supporting different subspecies were significant only at Frenchglen where sites occupied by A. tridentata ssp. wyomingensis had lower infiltration rates than A. tridentata ssp. vaseyana sites (fig. 3).

Differences in infiltration rates could, however, be partially explained by other site parameters. Surface soil and vesicular porosity

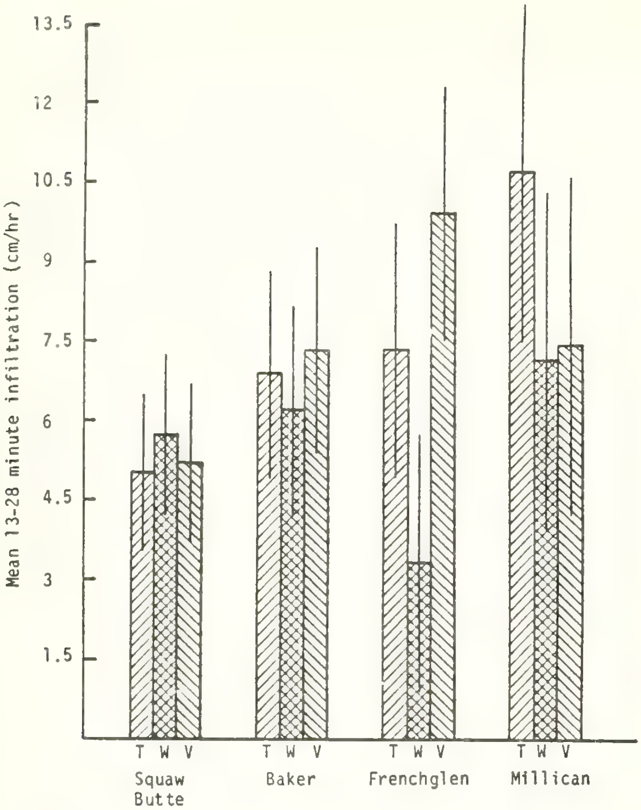

Figure 2.--Infiltration by location and subspecies. T = A. t. ssp. tridentata, W = A. t. ssp. wyomingensis, V = A. t. ssp. vaseyana. At a location, subspecies with nonoverlapping confidence intervals are significantly different at the 0.1 level of probability.

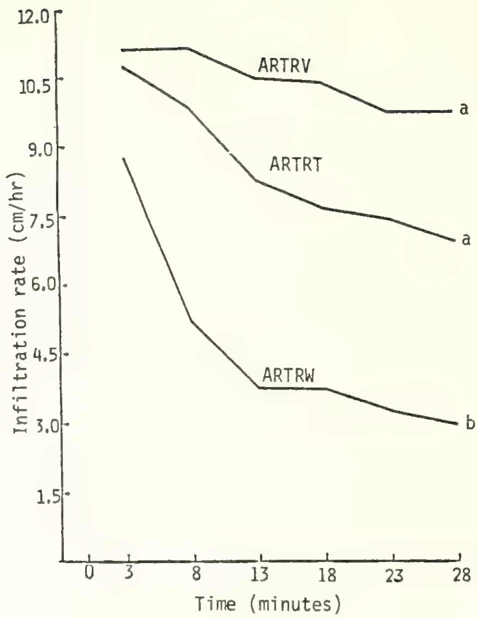

Figure 3.--Average infiltration curves for each subspecies at Frenchglen. Each line represents a total of 18 plots on three sites. The same letter at the end of two curves indicates a nonsignificant difference in infiltration rate during the last 15 mintes.

had lower rates of infiltration (fig. 4). Soils with loamy sand texture had significantly higher infiltration rates than soils with loam, sandy loam, or silt loam textures (inches/h 10.28, 6.62, 6.36, and 5.76 cm/h respectively). Although Borolls appeared to have higher mean rates of infiltration than other suborders, differences were nonsignificant between soil orders or suborders. Using stepwise multiple linear correlation, medium and coarse sand (0.25 to 2 mm) in the surface soil within each subplot accounted for 23 percent of the variability in average final infiltration rate (table 1). Combining organic ground cover with medium and coarse sand accounted for an additional 17 percent. Variables that were significantly correlated with final infiltration but did not improve multiple correlation included bare ground, clay, silt, bulk density, and organic matter. The amount of sodium in surface soils accounted for 11 percent of infiltration variability. Sediment concentration in runoff was also significantly related to infiltration (Swanson and Buckhouse 1984).

Five sites at the Millican location with surficial deposits of tephra had higher average final infiltration rates than the other 31 sites (3.58 and 2.56 inches/h, 9.1 and 6.5 cm/h respectively).

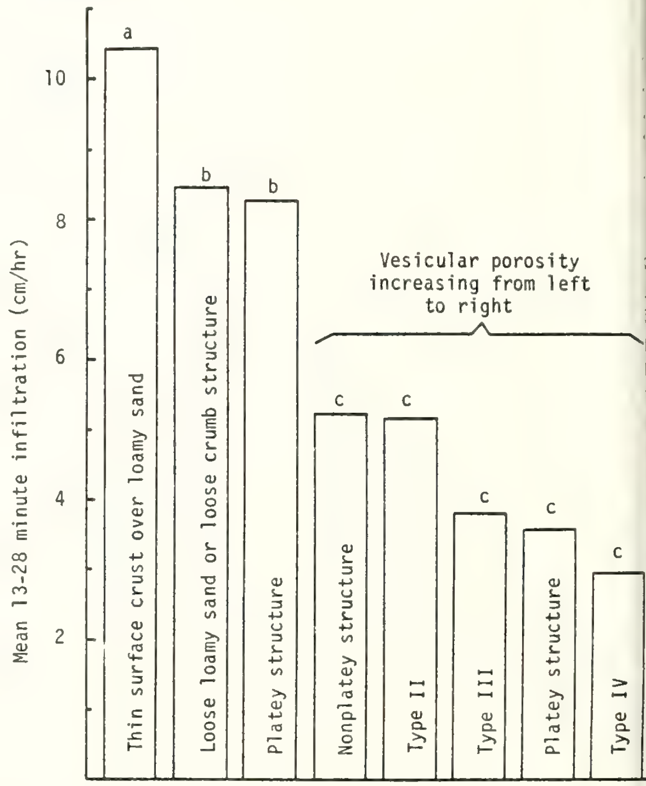

Figure 4.--Surface soil morphology and infiltration. Types II, III, and IV were described by Eckert and others (1977). Type II has many well-developed cracks; Type III has fewer well-developed cracks; and Type IV has few narrow cracks. Surface soil morphological types with differenct letters are significantly different at the 0.1 level of probability as determined by Scheffe's test.

Table 1.--Correlation analysis of soil surface and surface soil factors in 633 subplots with average final infiltration rate

Site factor	Stepwise Multiple R^2	Simple r
Medium and coarse sand (0.25 - 2mm)	Step 1 = .23**	.48**
Organic ground cover	Step 2 = .40**	.40**
Fine sand (0.05 - 0.25mm)		-.05NS
Bare ground		-.35**
Clay (<0.002 mm)		-.34**
Silt (0.002 - 0.05 mm)		-.27**
Bulk density		-.26**
Organic matter		.11**
Coarse fragments (>2 mm)		.01NS

**Indicates significance at the 0.01 level of probability.

Because of this difference, data analysis was repeated with these sites omitted. In that analysis, both soil order and suborder were significant descriptors for explaining infiltration rate. Mollisols had higher infiltration rates than Aridisols (2.8 and 2.08 inches/h, 7.25 and 5.29 cm/h respectively). Borolls had higher infiltration rates than Orthids (3.91 and 2.06 inches/h 9.94 and 5.23 cm/h respectively). In stepwise multiple linear regression, organic ground cover accounted for 29 percent of the variation, and percentage coarse fragments in the surface soil added just about half a percent to the multiple R^2. Surface soil morphology and habitat type analyses were essentially unchanged.

DISCUSSION

Shrub canopy zones generally have higher rates of infiltration than shrub interspaces because of differences in soil morphology, organic matter, and surface litter cover (Blackburn 1975; Brock and others 1982). This study, which examined infiltration in the shrub interspaces, can be taken as an indication of the response of the least absorbent parts of the site, but not of the site as a whole.

It was interesting to note that only at Frenchglen, which had the largest elevational difference among subspecies sites, was there a significant difference in infiltration rate among subspecies. Perhaps a wider and more representative elevational range elsewhere would have had study-wide significant differences in infiltration rates.

Regression analyses that included tephra sites supported the work of Rauzi and Kuhlman (1961), who found more rapidly declining infiltration rates on fine-textured soils. All correlation analyses, but especially the one omitting the tephra sites, support the conclusion that organic ground cover promotes infiltration (Branson and Owen 1970; Lang 1979; Meeuwig 1970). This relation between infiltration and organic ground cover may partially explain the higher infiltration rates found on Mollisols and especially Cryoborolls which have more organic matter in their surface layers. Increased organic matter can contribute to aggregate stability and a soil structure that is generally more favorable to infiltration. Soils with vesicular porosity are generally low in organic matter and are more frequently Aridisols.

The correlation of sodium with decreased infiltration may be an indication of the clogging effect of easily detached soil particles released by the dispersing action of sodium (Singer and others 1982).

Vesicular porosity occurs when air bubbles deform soil pores; hence it is an indication of soil instability under nearly saturated conditions. Infiltration rate can be reduced in these soils, as this and other studies have found (Blackburn 1975; Eckert and others 1977), because low aggregate stability leads to few surface pores and these are easily clogged by readily detached soil particles (McIntyre 1958). In addition, vesicular pores dampen the potential gradient by: (1) decreasing the soil particle surface area per unit volume; (2) increasing the depth to which a given quantity of water must penetrate before being absorbed; and (3) increasing the distance between the soil surface and the wetting front over which soil potential forces must pull.

Winward (1970) found that the occurrence of particular subspecies of big sagebrush did not correlate with soil texture. With this in mind, average infiltration rates in the last 15 minutes were adjusted using percent medium and coarse sand as a covariable. Even with this adjustment, tests for differences by subspecies, location, and condition class were nonsignificant.

CONCLUSIONS

The distribution of vegetation and process and infiltration are interdependent and controlled by many of the same factors. This correlation may aid managers in their attempt to understand rangeland hydrology; however, this investigation

indicates that vegetation identification must remain only one of many tools. Subspecies of big sagebrush, taken alone, were not shown to be reliable indicators of infiltration rates. They reflected significant differences in only one of four locations and that location had large differences in elevation among sites occupied by *A. tridentata* ssp. *vaseyana* and *A. tridentata* ssp. *wyomingensis*. Observable site parameters that did relate to increased infiltration rates were the absence of vesicular porosity, loamy sand texture, and greater amounts of organic ground cover.

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BIOLOGY AND ECOLOGY OF SAGEBRUSH IN WYOMING:

I. SOIL CHARACTERIZATION AND RESEARCH METHODS

Herbert G. Fisser

ABSTRACT: Monitoring of vegetation, grazing, and environmental factors in semiarid regions of western Wyoming, USA, was initiated in 1960. Plant community dynamics data have been recorded annually at 41 locations for 21 years. This paper gives a general portrayal of the Wyoming research sites. The methods of sampling are described. The climate is continental, average annual precipitation is 9 inches (22 cm) and mean annual temperature is 44 °F (7 °C). Yield and cover data of herbaceous species were obtained primarily with transects of 20 1- by 1-foot (30- by 30-cm) quadrats. Shrub yield was obtained with a weight-unit-estimation procedure. Intensive phenodynamics monitoring was conducted for ten years at 12 geographically diverse sites. Productivity data were derived by a weight-unit index procedure. Soil profile description, precipitation, and temperature were recorded. Annual photographic records have been maintained. The ERHYM model and precipitation-yield index procedures have been tested.

INTRODUCTION

Most rangelands of Wyoming are dominated by shrubs (Beetle 1960; Porter 1962; Küchler 1964). In Wyoming the most common and widely-dispersed shrub is Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis). Mountain big sagebrush (A.t. ssp. vaseyana) and basin big sagebrush (A.t. ssp. tridentata) are common, but restricted to smaller areas (Beetle and Johnson 1982).

Wyoming shrub ranges have supported a viable cattle and sheep industry for over 100 years (Nelson 1898; Vale 1975; Kearl 1980). Livestock management and that of pronghorn antelope (Antilocapra americana), mule deer (Odocoileus hemionus), and elk (Cervus elaphus) populations must meet ever increasing land use competition and economic stress (Kearl and Freeburn 1980; Olson and Gerhart 1982; Heady 1984). Ecological research for sagebrush was addressed 40 years ago (Robertson 1947). Efforts by W. M. Johnson (1969) and K. L. Johnson (1978) exhibited increasing awareness of the importance of sagebrush rangelands to agricultural, wildlife, and energy development industries.

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These ecological studies were initiated in 1962 (Fisser 1962, 1963a). Various aspects of this research have continued to the present through cooperative support from the University of Wyoming Range Management Department and the Bureau of Land Management (BLM) (Fisser 1984a). A great variety of interests have been considered during the many years of monitoring on more than 100 locations encompassing the semiarid shrublands of western Wyoming.

The objectives of this and the following companion papers in this proceedings are: (1) to characterize sagebrush-related research in Wyoming, (2) to identify sagebrush response to grazing and chemical shrub control, (3) to show vegetation/precipitation trends with regression, and (4) to apply a hydrology-based forage production model.

DESCRIPTION OF RESEARCH SITES

Herbage production and cover were obtained primarily in the Big Horn and Wind River Basins of Wyoming. One location was a relic site near Thermopolis, WY, reported by Passey and Hugie (1962). All others were fenced exclosures of 2 to 6 acres (1 to 3 ha) that had been installed by the mid-1960's. Also included was an exclosure near Farson, WY, in the Little Colorado Desert and four exclosures south and west of Kemmerer, WY, on the Bear River Divide. Later, others were established to extend the geographic locations eastward toward Casper, WY, and southward toward Baggs, WY, and Manila, UT (Fisser and Kleinman 1974). Long-term herbage production data from five locations have been selected for presentation in this report (fig. 1).

Location and Geology

The name, county location, legal description, and year of establishment of each of the five research sites are given in table 1. Bud Kimball and Smilo occur in the Big Horn Basin; and the remainder occur in the Wind River Basin to the south. These basins formed during the Laramide Revolution beginning in late Cretaceous and extending through Eocene time. Regional uplifting of mountains, faulting and warping, and regional degradation and sediment deposition occurred during the Pliocene and Pleistocene, giving Wyoming its present unique ecology and high elevation (Love 1960).

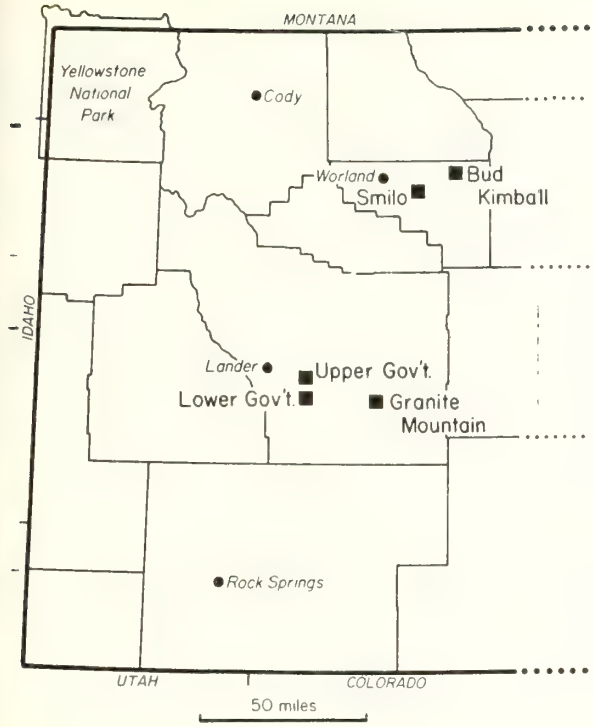

Figure 1.--Research locations in western Wyoming.

Soils and Topography

Soils are typical Aridisols derived under arid climates and exhibit poorly differentiated horizons. Most clay has been leached to lower horizons in the development process. Soluble salt concentrations are low and pH is well within tolerance ranges for growth of most species common to the sagebrush/grass region (Soil Survey Staff 1967; Ries 1973). Soil classification information is also given in table 1. Important differences in horizon thicknesses and textural values occur among sites; these affect soil moisture relationships (table 2).

Topography is generally level to slightly rolling with a general landscape of hills and plains. Slope values range from 0.5 to 5.5 percent. Exposures of the five sites are generally easterly from 30 to 110 degrees. Elevations range from 4,600 to 7,100 feet (1 400 to 2 160 m) (table 1).

Climate

The climatic region is continental, characterized by great diurnal and seasonal temperature variation, abundant sunshine, and mean annual precipitation of 8 to 11 inches (20 to 28 cm). Mean annual temperatures for the study sites were derived by extrapolation from nearby U.S. Weather Service Stations. Data extremes range from 110 °F (43 °C) in the Big Horn Basin to a low of -50 °F (-45 °C) at the Granite Mountain site in the Wind River Basin.

Table 1.--Location, general soil classification, and topographic information of the five research locations in western Wyoming

	Smilo	Bud Kimball	Lower Government	Upper Government	Granite Mountain
County	Washakie	Washakie	Fremont	Fremont	Fremont
Legal description TWSP	45N	46N	32N	33N	31N
RANGE	91W	89W	98W	97W	99W
SECTION	SWSE 14	NENW 29	NWSE 22	NWSW 32	NESW 7
Soil great group	Natrargid	Haplargid	Camborthid	Haplargid	Haplargid
Soil subgroup	Haplic	Ustollic	Borollic	Borollic	Borollic
Soil family (time)	Montmoril-lonitic mesic	Montmoril-lonitic mesic	loamy, mixed	loamy, mixed	loamy, mixed
Soil series	Absted	Ulm	Yamack	Almy	Forelle
Slope (percent)	5.5	2.0	0.5	0.5	0.5
Exposure (degrees)	076	110	085	080	030
Elevation (feet)	4,600	4,700	5,500	5,925	7,100
Elevation (meters)	1 400	1 430	1 675	1 805	2 165

Daily weighted mean seasonal temperatures of U.S. Weather Service Stations nearest each exclosure location are presented in table 3. On-site recorded seasonal precipitation was greatest during winter and spring (table 4). Although amounts vary from year to year, summer and fall precipitation occur consistently. This represents a major climatic variation from the Intermountain and Pacific Northwest region west of the Continental Divide where precipitation is almost completely absent during summer/fall, is greater in winter than spring, and where winter temperatures are adequate for early growth.

Vegetation

According to Küchler (1964) the sites in the more northerly Big Horn Basin occurred in the wheatgrass-needlegrass shrub steppe zone (*Agropyron-Stipa-Artemisia*). Those in the Wind River Basin occurred in the sagebrush steppe zone (*Artemisia-Agropyron*). The two categories were combined by West (1983) because of the small area of the former and because adequate literature was unavailable.

Wyoming big sagebrush and basin big sagebrush are the dominant shrubs (appendix I). Another frequently encountered shrub is Douglas or low rabbitbrush (*Chrysothamnus viscidiflorus*). The primary perennial grass is western wheatgrass; others include Sandberg bluegrass (*Poa sandbergii*), mutton bluegrass (*P. fendleriana*), prairie junegrass (*Koeleria cristata*), and needle-

Table 2.--Detailed physical and chemical soil charactersistics including textural class, bulk density, and porosity of the A and B horizons

	Smilo	Bud Kimball	Lower Government	Upper Government	Granite Mountain
Soil A horizon depth (inches)	0-4	0-5	0-3	0-3	0-2
Soil A horizon depth (cm)	0-10	1-13	0-8	0-8	0-5
Soil B horizon depth (inches)	4-11	5-8	3-11	3-16	2-17
Soil B horizon depth (cm)	4-28	13-20	8-28	8-41	5-43
Soil coarse sand (percent)	16.2	3.4	34.2	7.1	13.4
Soil fine sand (percent)	22.2	14.7	21.0	12.8	19.6
Soil silt (percent)	31.9	49.0	12.8	43.1	34.5
Soil clay (percent)	29.7	32.9	32.0	37.0	32.5
Textural class	clay loam	silty c.l.	sandy c.l.	silty c.l.	c.l.
Bulk density A horizon	1.3	1.6	1.3	1.2	1.1
Bulk density B horizon	1.7	1.5	1.7	1.6	1.5
Porosity (percent) A horizon	49	52	52	54	59
Porosity (percent) B horizon	37	42	35	38	44
pH A horizon	7.9	7.8	8.1	7.1	7.6
pH B horizon	8.3	7.9	8.5	7.4	7.5
Sol. salts A horizon (mmho/cm^2)	0.6	0.7	0.7	0.8	0.7
Sol. Salts B horizon (mmho/cm^2)	0.5	1.4	0.6	0.6	0.5
$CaCO_3$ A horizon (percent)	0.5	0.6	0.6	0.7	0.6
$CaCO_3$ B horizon (percent)	0.6	0.5	0.5	0.5	10.5

and-thread (Stipa comata). Additional perennial grass and grasslike species which occurred irregularly are bottlebrush squirreltail (Sitanion hystrix), blue grama (Bouteloua gracilis), Indian ricegrass (Oryzopsis hymenoides), and threadleaf and needleleaf sedge (Carex filifolia and C. eleocharis). The introduced annual cheatgrass brome (Bromus tectorum) on occasion responds with dramatic increase following sagebrush control but is usually limited by competition from associated perennial species, as is the native annual sixweeks grass (Vulpia octoflora). Common mat-form and succulents include Hood's phlox (Phlox hoodii), Hooker sandwort (Arenaria hookeri), plains pricklypear (Opuntia polyacantha), and rose pussytoes (Antennaria rosea).

History and Use

Trappers and explorers were familiar with what is now Wyoming early in the 1800's. The majority continued westward toward California and Oregon, but by the 1820's a number of trappers were living in the State. By the 1860's, immense numbers of cattle and sheep were being trailed into Wyoming from Texas and Oregon (Frink 1954). The Big Horn Basin, one of the last areas of the State to be settled, was bypassed by most emigrants and stockmen. In 1871, however, J. D. Woodruff began a cattle enterprise on the Owl Creek area and built the first cabin in the Big Horn Basin (Duhig 1948).

Table 3.--Mean daily temperature (°F) by season, taken from U.S. Weather Service Stations nearest each of the five research sites

Season	Number of days	Smilo Worland	Bud Kimball Tensleep	Lower Government Lander	Upper Government Sand Draw	Granite Mountain Jeffrey City	Mean
Winter	183	28	32	28	30	25	29
Spring	76	57	54	54	53	50	54
Summer	61	70	68	69	69	65	68
Fall	45	54	51	55	55	49	53
Mean*		44	45	43	44	40	44

* Adjusted and weighted for days per season

Table 4.--Long-term seasonal precipitation data for the five research locations in western Wyoming

Season	Smilo	Bud Kimball	Lower Government	Upper Government	Granite Mountain
	- - - - - -	- - - - - -	Inches	- - - - - -	- - - - - -
Winter October 16 - April 15	2.8	2.9	3.6	3.0	2.6
Spring April 16 - June 30	3.5	3.9	4.9	4.4	3.8
Summer July 1 - August 31	1.1	1.2	1.1	0.9	1.3
Fall September 1 - October 15	1.1	1.6	1.4	1.4	1.1
Annual	8.5	9.6	11.0	9.7	8.8

Little is known concerning the amounts and kinds of vegetation that were present during the early settlement years. In a diary written while traveling the Oregon Trail through the Wind River Basin, J. Dinwiddie wrote, "There is nothing but sand and sage" from the Sweetwater Crossing to South Pass, on the Wind River Range (Booth 1928). Generalized aspect, viewed in a similar context today, would not be much different. The disastrous loss of stock during the winter of 1866-67 is believed to have been the result of overgrazing as well as late spring storms (Frink 1954).

METHODS

Vegetation Monitoring

Introduction.--Earliest field research efforts, beginning in 1962, investigated vegetation cover and production of herbaceous species, primarily in the context of forage production. Area cover of all species was recorded. Only annual and perennial grass and grasslike species and single-stem annual and perennial forbs were clipped for determination of production. In 1971, study of biomass development of shrubs, mat-form, and succulent species was initiated with weight-unit-estimation procedures. In 1973, intensive studies were developed to record phenodynamics at 12 locations distributed from near Casper, Wamsutter, Manilla, Sage, Big Piney, Farson, and several locations in the Wind River and Big Horn Basins. Procedures to estimate community productivity were initiated in 1979.

Area cover and production.--Basal cover of herbaceous species and crown cover of shrub, half-shrub, and mat-form species, including the succulent plains pricklypear, was recorded (Fisser 1961; Fisser and Ries 1971). Area cover and herbage production studies on sagebrush-grass sites were conducted using transects of 20 quadrats, 1- by 1-foot (30- by 30-cm) spaced systematically along a randomly located 100-foot (30-m) steel tape. Cover percentages of all herbaceous, semiwoody, and woody species were estimated within each square foot unit. Data of shrub crown cover and basal cover of plains pricklypear, Hood's phlox, and Hooker sandwort were not combined when comparing area cover to herbaceous production since this group of plants was not clipped. Forage production was determined by clipping herbaceous species at ground or crown level at near peak standing crop. Exclosures were clipped on or near the same date each year. Clippings were oven dried at 158 °F (70 °C) for 24 hours prior to weighing.

Shrub production.--Beginning in 1971, shrub production was obtained by modified double-sampling during September and October. The technique involved a rapid weight-unit-estimation procedure. Estimates were made of transects consisting of 20 quadrats, 4- by 5-foot (1.2- by 1.5-m) spaced from 6 to 12 steps apart. The number of weight-units in each plot was estimated individually by two persons and then checked for accuracy. Weight-units were determined prior to the estimation procedure (Fisser and Ries 1972).

Phenodynamics.--To study the relationship of plant phenodynamics with vegetation production and environmental factors, an intensive monitoring program was initiated in 1973 at 12 research locations widely distributed in western Wyoming (Fisser and Kleinman 1974). Phenophase descriptions and stages were established for four primary species: western wheatgrass (*Agropyron smithii*), bluebunch wheatgrass (*A. spicatum*), big sagebrush (*Artemisia tridentata*), and black sagebrush (*A. nova*). A general phenology inventory scale was established for use on all other species.

Twenty individual plants of each of the four principal species were permanently located along 100-foot (30-m) lines in the 12 exclosures. Every 5 feet (1.5 m) on the line, directions along and from the line to the closest plant were recorded. Measurements of big sagebrush and black sagebrush included plant size, age, twig length, and seed stalk length. Measurements of western wheatgrass and bluebunch wheatgrass included plant size, age, leaf width and height, spike height, number of spikelets per seed head, and seed head development.

Separate scores were assigned for vegetative and reproductive development because plant individuals of semiarid regions seldom flower consistently. Time-lapse precipitation accumulation, maximum-minimum air temperatures, soil moisture and temperature, and site-characteristic photographs were recorded at each observation date (Fisser and Kleinman 1975).

Multiple step-wise regression was utilized to determine cause and effect relationships and correlations among environmental variables and plant development (Fisser and others 1977). In addition, a curvilinear regression model with a logrithmic growth curve and asymptotic limit was utilized to identify time-related phenologic development differences of species and life-form groups (Kinucan and Fisser 1984). These were then investigated to identify best plant predictors of climate variation.

Productivity.--Beginning in 1979, plant and community productivity relationships, with temporal and environmental changes, were studied using early- and late-season total population clipping and weight-estimation procedures. These were supplemented with multiple-period biomass sampling of individual culms and buds of the four prime species (Fisser and others 1980).

Beginning at least by the time of early standing crop estimation, individual plants of each prime species were clipped. Those selected represented the average phenology of a given prime species as indicated by the values of average phenology on the transect lines. The specimens to be clipped were selected at locations near the corresponding phenology transect line. At the first date each year, 40 specimens of each species were selected. Twenty were clipped and individually bagged with exclosure, species, and date identification. The remaining were identified with soft plastic-covered wire, placed on the ground in the case of

rasses and at the major twig base in the case of he sagebrushes. These were clipped at the next ampling date, at which time an additional set of 0 plants were identified with the soft, colored ire for subsequent sampling date clipping.

election of productivity units at the observation ime prior to the clipping date was incorporated nto the field procedures because of the intended xtrapolation of prime species productivity data o that of the plant community. Productivity easures of entire plant populations typically nvolve clipping all species at frequent intervals hroughout the growth season (Dickenson and Dodd 976). Such data provide estimates of total tanding crop at each date. They also require xtensive work force and time allocation equirements that are totally beyond the limits of he present study (12 locations geographically istributed over an area representing the western wo-thirds of Wyoming).

ith data for both early and midseason community standing crop, and with productivity data of four rime species at frequent intervals throughout the rowing season, essentially April through October, xtrapolation and interpolation can be utilized to xpress coefficients of weight-phenology related levelopment of the prime species to those of the community populations (Fisser 1984b). Thus, there ppeared to be an apparent conceptual need, when leveloping the present field procedures, for ime-extended relations of phenology-productivity nit selection and actual harvesting of the ndividual plants.

The procedures described in this report may not as closely depict true productivity values of community populations as clipping of all species would determine. The expression of standing crop at frequent intervals, derived from the productivity weight units integrated with early and late community standing crop, does provide, however, a valid characterization of community productivity dynamics (Fisser 1984c). In addition, the interrelation of prime species productivity units with phenologic progress will provide detailed description of phenodynamics and related standing crop values of these species (Fisser and others 1983)--data not available elsewhere that could be applied to the semiarid sagebrush-grass region typical of western Wyoming.

Time-variable environmental factors will influence both productivity and phenology. By interpretation of cause-effect responses, the biotic and environmental data will provide information useful for predicting growth and phenodynamics. Thus, future vegetation inventory processes can estimate probable crop production at any time during the growth season, subject to moisture and temperature benefits or restraints.

Productivity units of the wheatgrasses were individual culms. Selection was based primarily on the phenology average of the permanent transect lines. Height of culms, although uniform for most plants at a given stage of development, was specifically removed from the observer selection process.

Productivity units of the sagebrushes were individual twig tip initiation buds and initially included one node from the previous season's development. The inclusion of the added node was a minimal part of the productivity unit weight and was included to simplify the field procedure that required identification of a new bud twig as well as a uniform specified point at which it was to be removed from the shrub. The soft, colored wire was located at the base of the twig and did not affect bud growth development. Phenologic development, representative of the adjacent permanent phenology transect, defined the observer selection criteria. Length of current year twig development was used only if it related to identification of phenology that became definitive in some late-season reproductive stages (Fisser and others 1982).

Environmental Measures

Precipitation gauges with standard 8-inch (20-cm) orifice diameter were established at a few locations during the late 1950's (Fisser and others 1961). In 1960, and during subsequent years, smaller gauges were located at many research sites. A network of 70 gauges, spaced at 6 to 12 mile (10 to 20 km) intervals, was established initially throughout the Big Horn and Wind River Basins. A map with locations is given in Fisser (1963b). These gauges were metal cylinders with an orifice diameter from which 1 inch (2.54 cm) of precipitation would equal 100 ml (Fisser and others 1966). More than 200 gauges have been installed, primarily by the BLM, and are distributed over much of western Wyoming. Precipitation is recorded seasonally (Fisser and others 1966).

During the 1960's, a neutron probe was utilized to determine soil moisture (Fisser and others 1963). Gravimetric sampling with king tubes was conducted at several locations during the 1970's and early 1980's (Fisser and others 1977).

Ambient and time-lapse air temperature changes were recored with maximum- minimum thermometers. Soil temperatures at 1-, 8-, 15-, and 22-inch (2.54-, 20.35-, 38.1-, and 55.88-cm) depths were obtained from permanently placed thermographs (Fisser and others 1963). At sites of phenological studies, soil temperatures were obtained with thermometers inserted into the hole created by the king tube for soil moisture sampling (Kleinman and Fisser 1976; Fisser and others 1977).

Soil criteria were determined with the assistance of the BLM and the United States Department of Agriculture Soil Conservation Service personnel. Profile pits were excavated and characterized at all research locations. Samples were taken from each profile for detailed laboratory analysis (Ries 1973).

Photographic Record

Color and black-and-white photographs were taken to maintain a permanent visual record of research activities and temporal variation of vegetation and site conditions (Fisser and Ries 1973). A closeup photograph of each vegetation production transect and of those transects with permanent 1- by 1-foot (30- by 30-cm) quadrats was taken to show the first two quadrats. A general photograph was also taken showing distant vegetation and skyline. A single 2- by 20-foot (0.6- by 6.1-m) and 4- by 4-foot (1.3- by 1.3-m) quadrat for each exclosure characterizing grazing, chemical, and vegetation types was selected as a permanent photographic record site. Photographs were taken from one or more corners of each exclosure to provide visual expression of vegetation inside and outside the fenced units.

For 3 years during the phenodynamics study, closeup photographs of specific sagebrush branches, plains pricklypear clumps, and grass plants were taken at approximately 2-week intervals during the growing season. Observation of these segmental records exhibited a surprising characteristic in the production of reproductive stems. A specific branch usually alternated biennially, producing only vegetative growth one year, and producing seed the next (Kleinman 1976). Especially during years of moisture and temperature stress, it seems apparent that these shrubs are able to conserve their energy output related to development of reproductive structures and increase root components by restricting aerial growth to solely vegetative features.

Models and Forecasting

The generalized overview of modeling which has been approached in our research relates primarily to the water-balance climate model developed by Wight and Hanks (1981). In this model, which is identified by the acronym ERHYM, the herbage yields are determined as a function of the ratio of actual to potential transpiration values. Availability of input data, relative simplicity, and low computer costs make this model a viable tool for both research and resource management.

The major components of the ERHYM model require maximum and minimum temperature, daily precipitation and daily solar radiation climatic values. Soil information that is utilized includes albedo values of the soils, the water holding capacity, and infiltration rates. Daily update of soil water content is estimated by the model as related to the precipitation budget, evapotranspiration, and plant growth characteristics of the site. The vegetation components are identified by a crop coefficient and transpiration coefficient, as well as relative root distribution and a relative growth-curve factor. Growth is estimated on the basis of the ratio of potential evapotranspiration to actual evapotranspiration. The model integrates several aspects of range environment including amount of precipitation and daily distribution of precipitation. Evaporative demands of the vegetation are also taken into account. Soil moisture by horizon is a major factor and contributes to accurate prediction of rangeland yield.

The effectiveness of ERHYM depends upon its ability to simulate an accurate soil-water balance. Because there is little summer runoff a the sites in Wyoming, the soil-water components o the model were tested using single growing season runs in which actual, field-measured soil water values were used to initialize the model. Continuous runs were utilized to test the model's ability to predict over-winter recharge. For yiel predictions, the model is run in a continuous mod from 1965 through 1980 to match the available yield data. Overall, the ERHYM performed reasonably well on two sagebrush rangeland sites of western Wyoming. Additional validation trials are being conducted to determine the best crop coefficient and transpiration coefficient to improve the accuracy and long-term forecasting ability of the model. The results of this study indicate that the ERHYM model has a wide range of potential applications in research and management of semiarid rangelands.

Studies to determine the simple relationship of herbage production to precipitation were conducted. Many studies which attempt to show quantitative relationships of herbage yield with precipitation have generally been unsuccessful. This is due primarily to the variable temporal distribution of precipitation and the fact that range plants respond to soil moisture only during certain phenological stages and little, if any, during fall and winter in the northern United States. Use of seasonal or combinations of monthly precipitation have helped account for the distribution effects.

Since precipitation herbage-yield relationships often exhibit a very site specific dependency, the development by several researchers has involved the use of ratios of long-term values. A yield and precipitation index model for herbage yield, then, may be adjusted and forecasts can be made with some reasonable expectation of success. The analyses of Wyoming research site data show that the winter-spring precipitation gives the best overall prediction results. These analyses also suggested that combining the herbage yield from several locations gave most consistent results.

Whether a model can be utilized to predict and forecast vegetation interactions with differing climatic variables through time is dependent upon the quantitative characteristics of the model and of course, on the interpretative evaluation of those conducting the research. With long-term climate records and reasonably long-term data of herbage production, an accurate estimate of expected forage yield may be developed by those concerned with the ecology of semiarid rangelands.

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Appendix I.--Plant names, growth characteristics, and occurrence at the five research sites in western Wyoming by plant class.

Plant name	Plant class	Smilo	Bud Kimball	Lower Govt.	Upper Govt.	Granite Mtn.
I. Shrubs, half-shrubs, mat-form, succulent						
Machaeranthera glabriuscula	Half-shrub	X	X			
Artemisia tridentata ssp. tridentata	Shrub	X	X	X		
Opuntia polyacantha	Succulent	X	X	X	X	
Machaeranthera grindelioides	Half-shrub		X			
Gutierrezia sarothrae	Half-shrub		X			
Phlox hoodii	Mat-form		X	X	X	X
Haplopappus acaulis	Mat-form		X			X
Ceratoides lanata	Half-shrub			X		
Chrysothamnus viscidiflorus	Shrub			X	X	X
Antennaria dimorpha	Mat-form				X	
Phlox multiflora	Mat-form				X	
Antennaria rosea	Mat-form				X	X
Artemisia tridentata ssp. wyomingensis	Shrub				X	X
Leptodactylon pungens	Shrub				X	
Eriogonum ovalifolium	Mat-form					X
II. Perennial Grasses and Grasslike						
Bouteloua gracilis	Grass	X				
Sitanion hystrix	Grass	X		X		X
Agropyron smithii	Grass	X	X	X	X	X
Poa secunda	Grass	X	X	X	X	X
Stipa comata	Grass	X	X	X	X	X
Stipa viridula	Grass		X			
Koeleria cristata	Grass		X	X	X	X
Oryzopsis hymenoides	Grass		X	X		X
Carex eleocharis	Sedge			X		
Poa fendleriana	Grass					X
III. Perennial Forbs						
Crepis occidentalis		X				
Cryptantha bradburiana		X				
Castilleja angustifolia		X	X		X	
Cymopterus montanus		X	X		X	
Astragalus missouriensis		X	X		X	X
Machaeranthera canescens		X	X		X	X
Sphaeralcea coccinea		X	X	X	X	
Allium textile		X	X	X	X	X
Erigeron pumilus		X	X	X	X	X
Lomatium orientale		X		X		
Penstemon cleburnei		X			X	
Calochortus nuttallii			X			
Chaenactis douglasii			X			
Delphinium geyeri			X			
Lomatium simplex			X			
Sedum stenopetalum			X			
Zigadenus venenosus			X			
Viola americana			X	X	X	
Viola nuttallii			X	X	X	
Lewisia rediviva			X		X	
Musineon divaricatum			X		X	
Crepis modocensis			X			X

(con.)

Plant name	Plant class	Smilo	Bud Kimball	Lower Govt.	Upper Govt.	Granite Mtn.
Astragalus diversifolius				X		
Astragalus drummondii				X		
Oenothera caespitosa				X		
Oxytropis sericea				X		
Astragalus purshii				X	X	
Crepis acuminata				X	X	
Tragopogon dubius				X	X	
Agoseris glauca				X	X	X
Astragalus missouriensis				X		X
Gilia congesta					X	
Arabis holboellii					X	X
Lesquerella ludoviciana					X	X
Comandra pallida						X
Erysimum asperum						X
Erigeron compositus						X
Lithophragma parviflora						X
Lithospermum ruderale						X
Penstemon laricifolius						X
Penstemon eriantherus						X
Senecio canus						X
Trifolium gymnocarpon						X
IV. Annuals						
Androsace septentrionalis	Forb	X				
Salsola kali	Forb	X				
Machaeranthera tanacetifolia	Forb	X	X			
Vulpia octoflora	Grass	X	X			
Chenopodium leptophyllum	Forb	X		X	X	
Gilia pumila	Forb	X		X	X	
Plantago patagonica	Forb	X		X	X	
Plantago spinescens	Forb	X		X	X	
Bromus tectorum	Grass	X	X	X	X	
Descurainia pinnata	Forb	X	X	X	X	
Lepidium densiflorum	Forb	X	X	X	X	
Lappula redowskii	Forb	X	X	X	X	X
Sisymbrium altissimum	Forb	X		X		X
Chenopodium album	Forb		X			
Monolepis nuttalliana	Forb		X	X		
Collomia linearis	Forb			X		
Gilia leptomeria	Forb			X		
Mentzelia albicaulis	Forb			X		
Thlaspi arvense	Forb			X		
Microsteris gracilis	Forb			X	X	
Gayophytum ramosissimum	Forb			X	X	
Camelina microcarpa	Forb			X		X
Cordylanthus ramosus	Forb			X		X
Arabis lignifera	Forb				X	
Bromus japonicus	Grass				X	
Eriogonum cernuum	Forb				X	
Oenothera contorta	Forb				X	
Gymnosteris parvula	Forb					X

BIOLOGY AND ECOLOGY OF SAGEBRUSH IN WYOMING

II. GRAZING, SAGEBRUSH CONTROL AND FORAGE YIELD

Herbert G. Fisser

ABSTRACT: In conjunction with a 21-year aridland research effort in western Wyoming, effects of use of the herbicide 2,4-D and livestock grazing restrictions were evaluated at five research sites. Shrub reinvasion dynamics have been diverse. Early, rapid establishment was consistently related to beneficial growing season weather, intensive summer grazing, poor initial control, and increasingly mesic site character. Annual herbage production of sagebrush often increased with removal of livestock grazing. Grass and forb production always increased following sagebrush control and maintained increased levels throughout the life of the study.

INTRODUCTION

Big sagebrush (Artemisia tridentata) occurs over vast areas of western rangelands and is a dominant shrub on over 130 million acres (53 million ha) in the 11 western states. In Wyoming alone, big sagebrush covers more than 30 million acres (12 million ha) of rangeland (Beetle 1960). Historically, this shrub has been a prominent feature of the West. Reports of early travelers through the West, when much of the vegetation was presumed to be in pristine condition, indicate that sagebrush was very common and even a nuisance. Since those times, many believe that big sagebrush has prospered and expanded its range due to overgrazing by livestock (Ellison 1960; McArthur and others 1985).

This paper reports herbage production changes on basin big sagebrush (Artemisia tridentata ssp. tridentata) and Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis) rangelands aerially treated with 2,4-D (2,4-dichlorophenoxy acetic acid) in the butyl ester formulation. Herbage production was monitored on both treated and untreated native rangelands under grazed and deferred conditions. Data reported here encompass 20 years following the control of big sagebrush with this herbicide (Fisser 1984).

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The objectives of this study were to:
1. Evaluate sagebrush control practices.
2. Evaluate and compare long-term annual herbage production changes of (a) grazed and nongrazed treatments and (b) chemical control and natural treatments. 3. Interpret vegetation changes related to long-term effects of grazing exclusion and chemical treatment.

REVIEW OF THE LITERATURE

Sagebrush Distribution

Big sagebrush is the most widely distributed and abundant member of the group of woody shrubs collectively called sagebrush. It normally occurs as a dominant overshrub with understory of perennial grasses and forbs. It also grows in association with a variety of other shrubs such as bitterbrush (Purshia tridentata), serviceberry (Amelanchier alnifolia), and the rabbitbrushes (Chrysothamnus spp.) (Winward 1980). Although its volatile oils tend to make it unpalatable and may interfere with digestion, big sagebrush does, in many instances, provide high-quality forage for both livestock and wildlife. These volatile oils vary among subspecies, areas, seasons, and sometimes individual plants (Johnson 1976; Wallmo and others 1977).

Since the first identification of the species big sagebrush by Thomas Nuttall in 1841, three subspecies of this species have been recognized (Beetle 1960; Beetle and Young 1965). These three distinct subspecies are adapted to different growing conditions, but under some field conditions all may be found growing together (Beetle 1977).

Basin big sagebrush has probably the widest distribution and is the most common big sagebrush at elevations of 5,000 feet (1 500 m) and below (Winward 1980). It is an open, spreading shrub from 2 to 6 feet (0.6 to 1.8 m) tall and under favorable conditions can become treelike. This subspecies inhabits both wet and dry sites as well as strongly alkaline and nonalkaline deep-soil sites, but seldom occurs on shallow-soil sites (Beetle 1960; Beetle and Young 1965; Johnson 1976).

Wyoming big sagebrush is the most common big sagebrush in Wyoming and the most palatable of the subspecies. It is a dwarf shrub from 4 to 12

inches (10 to 30 cm) tall, found on dry, shallow-soil sites at medium elevations of 5,000 to 7,000 feet (1 500 to 2 130 m) in Wyoming. This subspecies is found with basin big sagebrush, but always occupies the poorer soil sites of hilltops and flats (Beetle and Young 1965; Johnson 1976).

The third subspecies, mountain big sagebrush (A. t. ssp. vaseyana), is the common big sagebrush at elevations of 7,000 feet (2 130 m) and higher. Characteristic growth form is a compact, flat-topped shape 1 to 3 feet (0.3 to 1.0 m) tall. Characteristic habitat sites are deep-soil, snow accumulation zones on mountain slopes (Beetle 1960; Beetle and Young 1965; Johnson 1976).

All three subspecies share characteristics of being long-lived perennial shrubs reproducing entirely by seeds (Brunner 1972). Growth starts later in the season than for most plants. Flowering does not take place until August or September and is a function of seasonal weather conditions, especially precipitation (Robertson 1971; Tueller 1973).

Much of the original range of sagebrush has been altered since the settlement of the West (Young and others 1979). Many thousands of acres of land have been plowed under and used for the production of agricultural crops. Other sagebrush ranges have been replaced by urban development, reservoirs, and transportation systems. The majority of sagebrush-dominated lands still exist, however, both under Federal (U.S. Department of the Interior, Bureau of Land Management and U. S. Department of Agriculture, Forest Service) and private ownership. The primary functions of these lands are for watershed protection, livestock production and wildlife habitat (Hedrick and others 1966).

Use of 2,4-D Herbicide

The discovery and development of the herbicide 2,4-D was documented by Peterson (1967). Many preliminary field studies were conducted. Findin supported allegations that 2,4-D uniformly kille broad-leaved weeds. After this, there was a dramatic increase in the marketing and use of 2,4-D as a herbicide. In 1962, it was used in Vietnam for chemical warfare, 20 years after initial studies and following widespread use to benefit agriculture. Several formulations of 2,4-D can be produced for use as herbicides or growth regulators. It can be obtained as an emulsifiable acid, amine salts, mineral salts, or esters (Klingman and Ashton 1975). The 2,4-D ester is the herbicidal form most commonly used for spraying big sagebrush.

Ester formulations of 2,4-D are generally considered to be the most toxic because:(1) volatility permits absorption of the gases throug stomata, and (2) wetting action of the oil-like ester and oil carrier translocation of the chemical is also greatest during rapid growth whe large amounts of food are being translocated and stored in the roots (Klingman and Ashton 1975).

Susceptibility of big sagebrush to 2,4-D was firs demonstrated in 1946 and 1947, just after the chemical had been introduced to the market (Cornelius and Graham 1951). The first test in Wyoming stemmed from a cooperative effort between the U. S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station and the Bureau of Land Management (BLM) in 1949 (Hull and Vaughn 1951; Johnson 1958). These tests proceeded on rangeland sites southeast of Lander, WY. From 1965 through 1976, as shown in table 1, almost 2 million acres (800 000 ha) of big sagebrush rangeland were sprayed in Wyoming (Freeburn 1978).

Table 1.--Total acres of sagebrush sprayed in Wyoming by federal agencies and individuals, 1953-1976 (Freeburn 1978)

Year	Ranchers in coop. with ASCS [1]	Bureau of Land Management	National Forests	Great Plains cooperative program	Private [2]	Total
1965	81,838	34,942	6,800	9,124	9,063	141,76
1966	76,760	54,929	3,276	1,714	7,505	144,18
1967	123,861	37,510	2,740	5,584	11,728	181,42
1968	96,601	27,808	1,331	8,607	18,345	152,69
1969	96,573	22,558	8,659	8,875	10,339	147,00
1970	92,036	11,290	11,390	27,805	17,643	160,16
1971	95,000	1,000	1,571	18,143	16,716	132,43
1972	99,057	0	0	25,339	11,032	135,48
1973	45,299	0	1,130	17,909	16,605	80,94
1974	22,873	0	0	22,263	15,680	60,81
1975	69,199	3,850	0	15,111	10,678	98,83
1976	0	0	0	20,082	0	20,08
Total	1,131,304	292,799	94,892	180,616	207,749	1,907,36

1 ASCS - Agricultural Stabilization and Conservation Service
2 Using minimum expanded estimate.

Although techniques for maximizing the percent kill of big sagebrush have been standardized, the ensuing herbage production, longevity of forage increases, and reestablishment of sagebrush have been highly variable among sites. On the areas sprayed in Wyoming during 1949 with a 97 percent sagebrush kill, the production of native perennial grasses exhibited a threefold increase in 2 years (Hull and others 1952).

This same study area, located 25 miles (40 km) southeast of Lander on the Beaver Rim, was the focus of analysis by another researcher. W. M. Johnson (1969) followed up the earlier studies to investigate long-term effects of chemical control on this site. These long-term effects were examined to determine longevity of the big sagebrush control project. Johnson indicated that the increased herbage production on the sprayed area was nullified 6 years after spraying and concluded that in this area the life expectancy of a big sagebrush chemical control project was 14 to 17 years.

Cornelius and Graham (1951) tested the susceptibility of big sagebrush to 2,4-D in 1948 on the Lassen National Forest in northeastern California. At an application rate of 1 pound (454 g) acid equivalent of the butyl ester in 20 gallons (75.7 L) of water per acre (0.4 ha) of land, 85 percent of the big sagebrush plants were destroyed. One year following spraying, production of the three major perennial forage grasses, Idaho fescue (Festuca idahoensis), western needlegrass (Stipa occidentalis), and bottlebrush squirreltail (Sitanion hystrix) increased 2.5 times over that on the unsprayed area. Also, reproduction of grasses on the sprayed area was over three times greater than on the unsprayed plots. The researchers were unsure if native grasses would recover as well in competition with a thick stand of the annual grass, cheatgrass brome (Bromus tectorum).

Another study with 2,4-D was initiated at the Squaw Butte Experiment Station, Burns, OR, by Hyder and Sneva (1956). In 1952, they applied 2,4-D butyl ester to a 40-acre (16 ha) pasture at 2 pounds (0.9 kg) of acid per acre (0.4 ha) on a site where the annual precipitation was nearly 11 inches (280 mm). However, in 1953, 15.68 inches (398 mm) of precipitation were received, stimulating an increased herbage production on the sprayed area of 3.25 times over that on the native range. In 1954, precipitation was recorded at only 6.77 inches (172 mm) while herbage yield was still three times that of the native range. It was suggested that increased grass production was not only due to a release from competition for moisture, but also from increased nitrogen availability. Many perennial grasses are much better competitors for moisture than big sagebrush, but the shrub has the advantage in competition for available nitrogen (Robertson 1947). Hyder and Sneva (1956) also found that individual grass species responded differently to sagebrush control measures.

A later study at the Squaw Butte Experiment Station compared the spraying of big sagebrush on both fair- and poor-condition livestock ranges (Hedrick and others 1966). Annual precipitation for a 20-year period was 11.8 inches (300 mm). For the 8 years of study, herbage yields on fair-condition range averaged 200 pounds per acre (224 kg per ha) for untreated ranges and 387 pounds per acre (434 kg per ha) for sprayed ranges. On the poor-condition range sites, herbage production averaged 122 pounds per acre (137 kg per ha) on untreated and 489 pounds per acre (548 kg per ha) on sprayed plots. On both sites, over 85 percent of the sagebrush plants were killed. Cheatgrass was the main source of the high yield on the poor-condition range plots. Herbage production for all plants fluctuated most on both the untreated and treated plots in poor range condition.

Alley and Bohmont (1958) discussed the results of big sagebrush spraying in 1952 with 2,4-D butyl ester. Their study sites were located in the Big Horn Mountains of Wyoming at an elevation of 8,200 feet (2 500 m), with an annual precipitation of 22 inches (559 mm). During their 5-year study period, air-dry native grass production increased fourfold from 526 pounds per acre (589 kg per ha) on the unsprayed to 2,075 pounds per acre (2 325 kg per ha) on the sprayed range (Alley 1965). These increases occurred where 75 percent or more of the big sagebrush had been killed. They also determined that livestock consumed 60 percent of available forage on sprayed sites and only 25 percent of the forage on unsprayed areas.

Fisser (1968) conducted a study to evaluate soil moisture, soil temperature, and herbage production changes following chemical control of big sagebrush on two sites. One was a xeric site in the Big Horn Basin and the other a more mesic upland site in the Wind River Basin of Wyoming. During the 5-year study, herbage production following chemical control increased on both sites and was greatest on the mesic site. Soil moisture withdrawal rates were similar at both sites, but less moisture was taken from the grazed treatment locations than from the nongrazed protected areas. High soil water withdrawal rates and cool soil temperatures following chemical control, combined with protection from grazing, were also related to an increased root abundance associated with the treatments (Orpet and Fisser 1979; Sturges 1980).

Response of vegetation and soil water to sagebrush control was reported by Sturges (1983) for a study site near Saratoga, WY, at an elevation of more than 7,000 feet (2 130 m). Productivity of mountain big sagebrush on 2,4-D sprayed sites was nearly twice that of the untreated areas 10 years after treatment. Sagebrush mortality was 96 percent. Sagebrush control clearly modified the soil water regime. Sagebrush reestablishment, however, appeared to have a minimal influence on the soil water regime for 11 years following treatment.

A survey of big sagebrush control projects in Wyoming was completed for the years 1952-64 by Kearl (1965). He ascertained that the length of life of a spray project was regulated by the percentage of sagebrush controlled and the management practices after control. Life expectancies for areas sprayed between 1952 and 1957 were estimated at 15 years while sites sprayed between 1958 and 1960 revealed life expectancies of only 10 years. Later control programs, with improved methodology, resulted in potential effective life spans of 30 to 40 years. His survey reported forage increases ranging from 0 to 400 percent, with most common increases between 100 and 200 percent (Kearl 1973).

DESCRIPTION OF STUDY AREAS

During the late 1950's and early 1960's, trials to test the ability and requirements for control of sagebrush with the chemical 2,4-D were initiated at a number of locations in the Big Horn Basin, Wind River Basin, and areas near Kemmerer, WY (Fisser and Whysong 1969). Five separate areas, all located in Wyoming and on BLM lands, were selected for discussion in this report. Exclosures were erected on these sites to monitor the effects of livestock grazing and exclusion on the chemically controlled and native vegetation. These exclosures, Smilo, Bud Kimball, Lower Government Draw, Upper Government Draw, and Granite Mountain, were constructed by the BLM. They are located in north-central and west-central Wyoming (fig. I-1, Fisser, this proceedings). The soils of the study sites are all typical of those derived under arid climates (aridisols), and exhibit poorly differentiated horizons. Salt concentrations are low and pH is within the tolerance range for the growth of most sagebrush-grassland species (Ries 1973).

The immediate topography of these sites is generally level to moderate to gently sloping while the overall landscapes are rolling hills and plains. Slope values range from 0.5 percent to 5.5 percent on exposures of 30 to 110 degrees. Elevations vary from 4,600 feet (1 400 m) at the Smilo site to 7,100 feet (2 160 m) at the Granite Mountain site. Bud Kimball, Lower Government Draw, and Upper Government Draw exist at elevations of 4,700 feet (1 430 m), 5,500 feet (1 676 m), and 5,925 feet (1 805 m), respectively. Greater detail of site characteristics is given in the first paper of this series (Fisser, this proceedings).

METHODS

The exclosures were constructed by the BLM during the summers following early June application of herbicide. In the Wind River Basin, two exclosures, Lower Government and Upper Government, were treated and established in 1958. The two Big Horn Basin exclosures, Smilo and Bud Kimball, were completed in 1961. The Granite Mountain exclosure in the Wind River Basin was treated and installed in 1962.

The herbicide 2,4-D butyl ester was strip-spraye by air under the supervision of the BLM. The chemical was applied in a mixture with diesel oi at the rate of 2 gallons per acre (18.7 L per ha Precipitation was recorded seasonally on April 1 July 1, September 1, and October 15 with gauges each location.

Research on grass and forb production by the University of Wyoming was initiated in 1962, whi shrub production studies began in 1968. Living herbaceous plant material was clipped at or near peak growth for the purpose of estimating annual production. All the study plots of grasses and forbs were clipped (Fisser 1963).

Grasses and forbs were sampled in 20 1- by 1-foo (30- by 30-cm) quadrats located at 5-foot (1.52- intervals along a 100-foot (30-m) tape (Fisser 1963). These tapes were located on all treated and untreated sites by a restricted random proce so as not to coincide with lines of previous years.

Shrub biomass was sampled at a later date than grasses and forbs since most shrubs, including b sagebrush, exhibit maximum yearly growth at a later time. For estimation of shrub production, modified double sampling method was employed (Fisser and Whysong 1969). A 4- by 5-foot (1.2- by 1.5-m) quadrat was used. Twenty quadrats wer located at 6-pace intervals along a randomly located line within each of the treatment areas (Fisser 1968).

Photographs of all lines were taken prior to collection of data. Percent cover for all individual species of grasses and shrubs was estimated within each quadrat prior to clipping separately by species. Vegetation samples were ovendried at 158 °F (70 °C) for 24 hours.

ANALYSES

Data from the five research locations were combined for presentation in this report. Simpl linear regression was used to determine the seasonal precipitation groups which most closely related to vegetation dynamics. Vegetation class subjected to analysis were annual yield of perennial grasses, all grasses and forbs, all species, and big sagebrush. These records were compiled for each of the treatment combinations: 1. native-nongrazed, 2. native-grazed, 3. shrub control-nongrazed, and 4. shrub control-grazed. The t test of paired means for years was used t compare all combinations of long-term yields amo grazing and chemical shrub control treatments fr the five research locations.

RESULTS

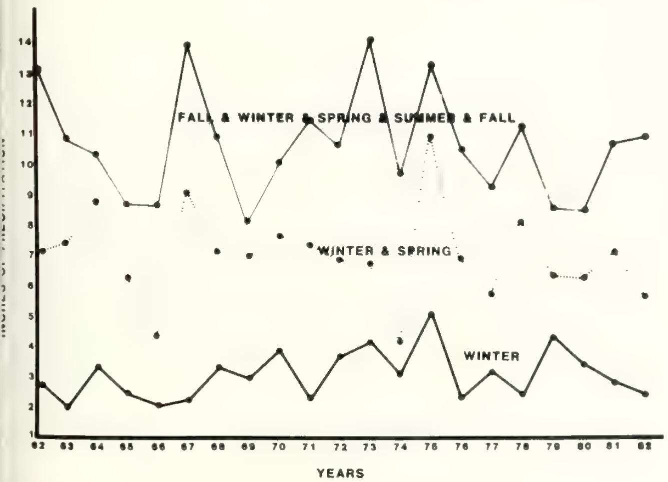
Two kinds of information will be presented in th report. The 21-year precipitation record and long-term yield data, with appropriate quantitative analysis, will be analyzed for the five research sites combined. Secondly, the general nature of the five exclosures identified

n the previous report will be descriptively haracterized. The narrative will present a iscussion of vegetation responses to the grazing reatment, the chemical shrub control treatment, nd interactive environmental variables. It has een readily apparent over the years that annual onitoring is necessary because of dynamic egetation response to treatment impacts and nvironmental changes. Without annual data ccurate interpretation of interactive responses ould not be possible.

rouped Site Analysis

recipitation.--The 21-year record of recipitation presented in figure 1 identifies hree seasonal periods most closely related to egetation yield, combined over the five sites. ean total winter plus spring precipitation was .1 inches (180 mm)(table I-4, Fisser, this roceedings) with standard error of 1.52 inches 38.6 mm). Yield of perennial grasses and forbs as most closely related ($p < 0.001$) to the sum of inter plus spring precipitation. Mean annual alues ranged from a low of 6.42 inches (166 mm) t Smilo, to a high of 7.14 inches (181 mm) at pper Government. The similarity of these data mong the five sites is an expression of overall limate control induced by the mountains of the ontinental Divide to the west. The Big Horn asin sites were, in general, more xeric than hose to the south in the Wind River Basin. ariation among years, however, can result in any ne of the sites receiving greatest precipitation Ries 1973). No temporal trend in any of the easonal precipitation groupings was discernible.

he precipitation for the winter season, October 6 to April 15, was next most closely related to erbage yield, more so than the spring recipitation by itself. Although 32 percent of ean annual precipitation occurred during the inter (table I-4, Fisser, this proceedings), tandard error of the mean was only 0.82 inches 21 mm). Spring moisture provided 43 percent the otal, 4.1 inches (104 mm), but exhibited much reater annual variation; standard error of the mean was 1.46 inches (37 mm). Winter precipitation for the 21 years on the five sites averaged 3.0 inches (76 mm). Lowest mean annual value was 2.85 inches (72 mm) at Smilo, and the highest at Lower Government was 3.43 inches (87 mm). Somewhat surprisingly, winter precipitation at Granite Mountain was similar to that at Smilo, while Bud Kimball and Upper Government were intermediate and considerably less than at Lower Government (Fisser 1984).



igure 1.--Mean precipitation (inches) of five estern Wyoming research locations, for 21 years, ompiled for three seasonal categories.

The mean annual plus current fall precipitation was 10.63 inches (270 mm) with standard error of 1.76 inches (45 mm). Lowest mean annual value was not at Smilo as for the previous categories, but at Upper Government, with 9.11 inches (231 mm). This obviously was an expression of lesser amounts of fall and summer precipitation at this location than at the others. Greatest precipitation was recorded at Lower Government with 11.65 inches (296 mm). The precipitation value of this five-season period--previous fall, winter, spring, summer, current fall--was useful because of the strong relationship with total biomass of all species, and especially with that of shrub species. The latter, because of deep root systems and late summer-early fall maturation, were able to use deep water from previous fall and winter occurrences and from the current year's fall moisture because their yield was obtained during the fall period.

Vegetation.--In this report the mean annual yield of perennial grasses is used to show response, over time, to the grazing and chemical shrub control (spray) treatments. The nongrazed sites yielded 155 percent of the grazed (fig. 2). The shrub-controlled sites yielded 171 percent of the unsprayed.

The mean annual production of perennial grasses at the five sites, for 21 years, is shown for each of the four treatment combinations in table 2. The t-test of paired mean differences was highly significant ($p < 0.001$) for all comparisons except for the differences between grazed-shrub control and nongrazed-untreated, which was, however, significant at $p \leq 0.1$.

Table 2.--Mean annual yield (pounds per acre) of perennial grasses by grazing and chemical treatments at the five western Wyoming research locations

Treatment	Mean yield	Group means	Stand. error of the mean
Grazed - unsprayed	168		8.56
Nongrazed - unsprayed	216	192	13.48
Grazed - sprayed	239		12.84
Nongrazed - sprayed	416	328	20.44

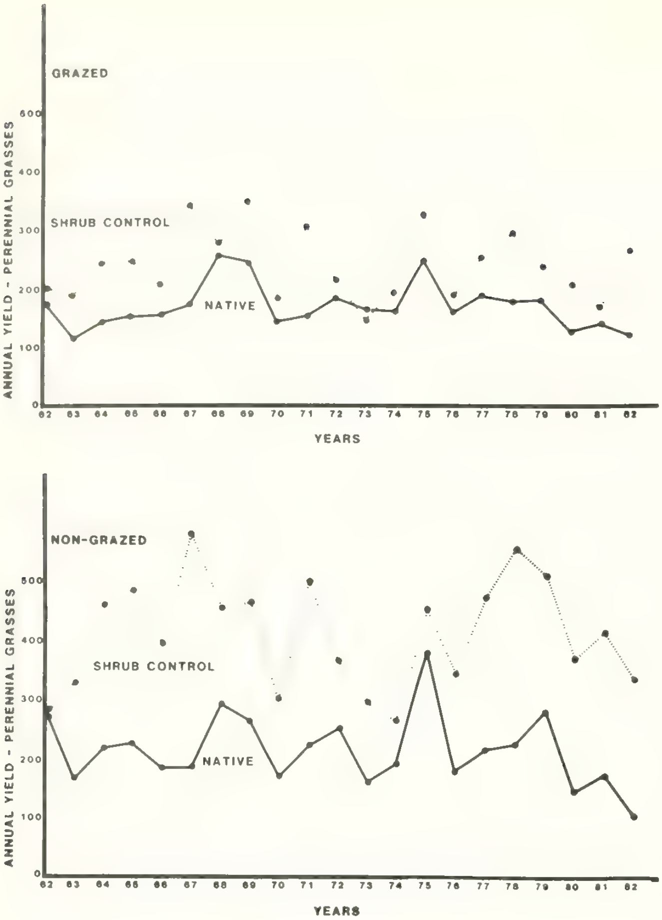


Figure 2.--Mean annual perennial grass yield (pounds per acre), for grazed (above) and nongrazed (below) treatments of five research locations in western Wyoming.

Changes with years were relatively similar among the five sites. Greater variation of yield over years occurred under the nongrazed treatment, however, showing that the moderate use noted on these sites did tend to inhibit herbaceous response (fig. 2). The yield dynamics of the nongrazed-sprayed sites were much greater than any of the other three treatment combinations. This would be expected in light of freedom from the influence of shrub dominance and release from grazing stress (Hedrick and others 1966).

Although some reinvasion by sagebrush, primarily on the intensively grazed sites, was evident, the high perennial grass response to the chemical shrub control treatment has been maintained. The trends exhibited in records extending well over 20 years beyond the chemical application indicate that beneficial effect, as suggested by Kearl (1973), may well persist for as much as 40 years. Continued monitoring of interactive environmental, grazing, and chemical treatment relations will be necessary to determine how long the shrub control impacts and benefits continue (Winward 1980). It is apparent that changes caused by chemical shrub control are long-term, at least on the semiarid sagebrush rangelands investigated in Wyoming.

Individual Site Characterization

Smilo exclosure.--The Smilo site is the most xeric and warmest during summer of the five selected locations. Although lower growing than normal in its more common occurrences along drainage sites, the dominant shrub is basin big sagebrush (fig. 3). Poor ecological condition wa apparent in 1961. Very little perennial understory existed then. The most important perennial grasses are western wheatgrass (Agropyron smithii), blue grama (Bouteloua gracilis), bottlebrush squirreltail (Sitanion hystrix), Sandberg bluegrass (Poa secunda) and needleandthread (Stipa comata).

The response of perennial grasses to protection from grazing has been extremely limited. Initial response to chemical shrub control was positive but was severely restricted by a climatically induced population explosion, coincident with long, warm, moist, spring and moist, summer weather, of the annual cheatgrass in the mid-1960's. Striking differences between the unsprayed and chemically controlled sites have persisted. The nongrazed sagebrushes, especially in the chemically treated site, were vigorous. Some exhibited enhanced growth and reproduction, but they did not reestablish in abundance. Total grass and forb production on both untreated sites remained relatively stable. Precipitation was a dominant factor, as was the eroded soil of the site. The cheatgrass explosion indicated that shrub control practices should be restricted to better condition rangelands, at least if ecological condition increase is a primary goal. Very long-term beneficial values may be obtained on these sites, however, with stabilization of soils.

Figure 3.--The Smilo exclosure southeast of Worland was in low ecological condition, with abundant annual weeds, in 1961.

Bud Kimball exclosure.--Basin big sagebrush, as at Smilo, is dominant at the Bud Kimball exclosure (fig. 4). Ecological condition was fair at the time of establishment. The most prominent grasses were western wheatgrass and sandberg bluegrass. Others of lesser importance were Indian ricegrass (Oryzopsis hymenoides), junegrass (Koeleria cristata and needleandthread. Good chemical control, better ecological condition, and greater site potential than at Smilo resulted in positive response to protection from grazing and the chemical treatment (fig. 4). Cheatgrass did not become a dominant. Sandberg bluegrass and western wheatgrass increased significantly after shrub control, and moderately with protection from grazing. Bluebunch wheatgrass (Agropyron spicatum) did become established in a corner of the exclosure but was never encountered during sampling for vegetation yield. Increased sagebrush was evident on the shrub control site by 1980, but perennial grass yield was little affected. Yield was much more responsive to precipitation dynamics than at the xeric Smilo site.

Lower Government exclosure.--The basin big sagebrush dominant at the Lower Government (LG) site is almost 3 feet (1 m) tall and exhibits typical characteristics of growth on sandy soil with a relatively shallow permanent aquifer (fig. 5). Western wheatgrass is the most prominent grass on native range. Needleandthread exhibited striking response to the combination of protection from grazing and chemical shrub control. Sagebrush inside the exclosure, especially a few bushes remaining in the shrub control area, exhibited good growth while those outside the exclosure had a hedged appearance. Protection from grazing induced only moderate response of understory perennial grasses because of the dominant influence of big sagebrush.

As at Smilo, wheatgrass was most abundant on the sprayed area protected from grazing. It contrasted, however, in that the initially better ecological condition, greater site potential, and cooler summer temperatures favored dominance by perennial grasses. Outside the exclosure, because of damage to sagebrush from animal trailing and minimal perennial grass presence, cheatgrass was more abundant than on the nearby grazed sprayed site. Even under intensive grazing, perennial grass yield on the treated site, in contrast to the xeric, low condition Smilo site, was adequate to restrict cheatgrass and other annuals.

The perennial grasses continued exhibiting strong interspecific competitive response after sagebrush became rather abundant. Even when the physiognomic aspect of the herbicide-treated site was essentially identical with that of the nonsprayed range, understory perennial grass and forb yield, cover, and density maintained beneficial effects of the chemical treatment throughout the study period.

Upper Government exclosure.--Wyoming big sagebrush is dominant at the Upper Government exclosure (fig. 6). Protection from grazing produced little vegetation change except when compared to sites of extreme overuse. Vegetation composition is significantly different from other rangelands in that junegrass is the most common understory species. Other species of lesser importance are western wheatgrass, Sandberg bluegrass and needleandthread. The continued abundance of junegrass on untreated range occurs as a result of site potential for multiple climax expression and the stability of vegetation on these sites dominated and controlled by sagebrush (Heady 1973).

Figure 4.--The Bud Kimball sagebrush control site protected from grazing showed abundant perennial grass yield and little sagebrush invasion even in 1981.

Figure 5.--Lower Government exclosure of basin big sagebrush showing limited reinvasion.

Figure 6.--Intensive use of grasses at the Upper Government exclosure, primarily junegrass, in the foreground, and generally reduced size of Wyoming big sagebrush bushes, is apparent. Greater sagebrush invasion is evident on the grazed-sprayed strip.

Yield of perennial grasses and forbs was much greater on the 2,4-D treated site than on the untreated range. With removal of sagebrush, grass composition has begun shifting from an overriding dominance by junegrass to needleandthread. Annuals were never abundant.

Shrub yield was similar for the unsprayed sites, both ungrazed and grazed. Protection from use allowed cover and growth of sagebrush plants to increase in contrast to the minimal changes on the grazed site. Livestock and wildlife effectively inhibited sagebrush because of browsing and mechanical damage. Under the herbicide treatment sagebrush yield was similar, whether grazed or not, but density increased during later years as a result of grazing stress and reduced competitive ability of herbaceous species.

Herbage yield fluctuations, as a result of changing growing conditions, were greatest on the sprayed site and on the area protected from livestock use. Sagebrush presence effectively limited herbage response to beneficial moisture and temperatures. Where sagebrush reinvasion was noted, perennial grass and forb yield was still greater than on the unsprayed areas.

Granite Mountain exclosure.--While the Wyoming big sagebrush was very effectively controlled at the Upper Government exclosure, a rather poor kill was obtained at the Granite Mountain exclosure (fig. 7). As a result, reinvasion of the shrub was more evident and rapid than at other locations. Partially killed shrubs began rapid growth within a few years inside the exclosure, but density increase was only moderate. Outside the exclosure sagebrush response following spraying was expressed primarily by density increase, as growth and size were inhibited by livestock and wildlife impact. Sagebrush size and density changed little on the grazed-nonspray sites. Those inside the exclosure, however, exhibited more seedheads and longer stems than those of the grazed area, an evident result of protection from livestock and pronghorn antelope.

Mutton grass (Poa fendleriana) was a dominant at this site, evidently in response to somewhat greater summer precipitation and cooler summer temperatures than at any of the other locations. Deeper B horizon, good porosity, low bulk density, and pH of soil all contributed to a vegetation complex similar to that of foothill sites with much greater precipitation than at the Granite Mountain location.

Perennial grass and forb yields changed little over the years on the untreated shrub-dominated sites, whether protected from grazing or not. With chemical shrub control, however, herbaceous species exhibited much increase, especially mutton grass, western wheatgrass, Sandberg bluegrass, and to some extent needleandthread. Greatest production increases occurred inside the exclosure of course. Summer cattle grazing occasionally severely inhibited growth outside the exclosure and apparently also was responsible for some sagebrush reinvasion.

This site has the highest yield potential of the five locations. Despite the weak sagebrush control, and partially because the site was in at least fair ecological condition when treated, annuals were never abundant. In addition, the positive response of perennial grasses to shrub control continued and appeared little influenced by the presence of sagebrush within the spray area of the exclosure. A similar, but less striking response of herbaceous species was also noted in the sprayed-grazed area outside the exclosure.

Figure 7.--At the Granite Mountain exclosure large and scattered Wyoming sagebrush bushes indicate poor chemical control, little intraspecific competition, but strong interspecific competition from perennial grasses.

[D]ISCUSSION

[R]esponse to protection from grazing, with no shrub [c]ontrol, was minimal in terms of understory [p]erennial grass and forb species. Sites of low [e]cological potential, and those in poorest [e]cological condition, exhibited weakest response. [C]onversely, sites of highest potential and better [e]cological condition responded well. Protection [f]rom grazing on untreated range allowed growth of [b]ig sagebrush plants that was not exhibited on the [g]razed sites. Grazing use on sagebrush outside [t]he exclosures was always evident.

[C]ontinued moderate grazing on untreated sites did [n]ot appear detrimental to herbaceous species. In [c]ontrast, the grazing allowed little vegetation [r]esponse by herbaceous understory species or by [t]he overstory shrubs, to potential benefits of [y]ears with good growing conditions. Whether or [n]ot big sagebrush is considered a climax dominant [o]n these sites, its present abundance effectively [c]ontrols herbage yield dynamics, and the removal [o]f grazing can hardly be expected to have [i]mmediate effects on these long-lived plants.

[B]eneficial vegetation response to chemical shrub [c]ontrol was most evident: (1) with protection from [g]razing, (2) on sites of highest ecological [c]ondition at time of treatment, (3) on sites with [g]reatest yield potential, and (4) when annuals [r]emained minimal components of vegetation [p]opulations.

[U]nless grazing use was destructive, the impacts [w]ere moderate, and in most situations provided [b]enefit to the perennial herbaceous species by [r]educing interspecific competition with annuals [a]nd reinvading shrubs. Sites in poor ecological [c]ondition required greater recovery time than [t]hose in higher condition. Dynamic herbage [p]roduction response is positively related to yield [p]otential. Sites of low yield potential often may [n]ot provide adequate returns from increased forage [t]o be cost-effective for a shrub control [t]reatment. However, the treatment can have a very [i]mportant long-term value in soil movement [r]eduction, that may well be much more important [t]han the minimal value associated with the limited [t]emporal vegetation yield changes.

[P]resence of annuals is more expected in the warm, [x]eric areas of the Big Horn Basin than in the Wind [R]iver Basin to the south. When poor condition, [l]ow potential, and invasion by annual weeds [c]ombine, the expected perennial grass increase [a]fter shrub removal can be minimal. In some [i]nstances the great herbage yield of annuals may [b]e used as forage, but the continued danger of [e]xcessive erosion persists.

[I]t is apparent that multiple pathways of [v]egetation succession exist. Even with almost [c]omplete removal of sagebrush and its controlling influence over the community, each of the study [a]reas exhibited site-specific species composition. [V]egetation components and consequent community dynamics, it seems, should be expected to show different paths toward climax. To assume that all must eventually achieve essentially uniform composition would, first of all, ignore the concepts of natural stability on these semiarid ranges. As noted by West (1985), the process of succession is real and can be described, but predicting the paths and dynamics of change is difficult. Secondly, each site exhibits some physical or chemical environmental characteristics not present at others. These often minor factors may differentially influence different plant species. Interactive response may be so minimal that most common field sampling procedures are unable to detect significance. Long-term abundance and lack of expected change according to typical or expected successional progression can be interpreted ecologically by general knowledge of unique growth characteristics of the vegetation and individual species.

SUMMARY AND CONCLUSIONS

Precipitation and herbage yield were monitored for 21 years at five locations in western Wyoming. Interactive responses to environmental influences, to grazing-nongrazing, and to chemical shrub control-no shrub control treatments, were investigated. Each of the five research locations exhibited unique physical, chemical, or biotic characteristics. Precipitation was surprisingly similar among the sites. Response to precipitation amounts and shrub control treatments by perennial grasses was highly significant.

Grazing generally caused only minimal stress and reduction to forage yield except for sites subjected to atypically extreme use. Protection from grazing did not, by itself, benefit herbaceous species adequately to be identified as a potential management plan.

Herbicide spraying caused very significant positive forage responses. These responses were, on occasion, limited by poor ecological range condition, low ecological potential, poor control of the shrubs, and continued intensive grazing. Beneficial effects of the spraying, at least in terms of increased perennial grass forage yield, are expected to persist for many years into the future. With moderate grazing these grasses can maintain abundance and yield in spite of competition from the perennial shrubs.

ACKNOWLEDGMENTS

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BIOLOGY AND ECOLOGY OF SAGEBRUSH IN WYOMING:

III. PHENOLOGY

Herbert G. Fisser

ABSTRACT: Phenology of sagebrush was recorded at 12 locations in Wyoming representing the Big Horn Basin, Wind River Basin, Shirley Basin, Little Colorado Desert, Red Desert, and the Bear River Divide from 1973 through 1982. The quantitative scoring system distinguished vegetative from reproductive development. Herbage production and phenology of all species were also obtained. Phenological "phase," "stage," and "substage" characterization terms and phrases were established for distinctive appearance changes and integrated with a numerical scale. Regionally related phenodynamic differences were irregular and basically controlled by climatic factors. The increased precision of phenological characterization, with potential for detailed phyllochron distinction, provides a sensitivity level more nearly equivalent to commonly measured values of environmental factors such as soil moisture and temperature, soil texture, ambient temperature, precipitation, and others.

INTRODUCTION

Most reports of phenodynamics commonly portray annual life cycles with flowering, seed set, and maturation. Many perennial species of semiarid communities, however, seldom consistently flower each year. Vegetative structures do usually complete the entire phenophase cycle, from growth initiation through senescence, even if reproductive structures fail to develop. Development of individuals or populations has been investigated, but little effort has been extended toward the phenodynamics of entire communities. Furthermore, few reports are available that quantitatively evaluate phenodynamic interactions within or among communities and with environmental variation.

This investigation of plant phenology was conducted in central and western Wyoming for 10 years, from 1973 to 1982, at 12 diverse locations, all dominated by big sagebrush (Artemisia tridentata)(Fisser and Kleinman 1974). Black sagebrush (A. nova) was present at several of the sites (Hargis 1980). The program was a cooperative effort between the U.S. Department of the Interior, Bureau of Land Management (BLM), and the University of Wyoming, Department of Range Management.

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The objectives of this study were to: (1) investigate both vegetal and reproductive phenologic patterns, (2) investigate whether these patterns were environmentally influenced, and (3) interpret these phenomona in an ecological context.

REVIEW OF LITERATURE

The term "phenology" is said to have been coined by the early botanist, Charles Morren (Lieth 1970). Henry David Thoreau has been credited as the father of phenology in the United States by Leopold and Jones (1947). Their work was exceptionally important because it identified regional phenologic variation as resulting not only from weather influences but also from integral genetic and site variation differences. Phenology has a variety of definitions. Newman and Beard (1962) described phenology as the art of observing life cycles in plants and animals. The U.S. International Biological Program Committee (Lieth 1974) expressed it as "the study of the timing of recurrent biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species."

The contemporary approach to phenology has become strongly oriented toward obtaining records with detailed descriptions of time sequences of plant development (Turner and Klipple 1952; Caprio 1966; Dierschke 1972; DePuit and Caldwell 1973; Dickenson and Dodd 1976; Kleinman 1976; Sauer and Uresk 1976). West and Wein (1971) proposed a digitized procedure to reduce the qualitative nature of phenology reporting and to approach interpretation with data more amenable to statistical analysis.

Big sagebrush was observed in Nevada by Robertson (1943). He noted that this shrub exhibited an early increase in photosynthetic activity from its winter dormant state that gave it a strong competitive ability for reinvasion of rangeland reseeded areas. Its root system gave the plant an opportunity to avoid short-term temporary growing season drought which caused severe stress to reseeded grasses with shallow and less comprehensive root systems (Brunner 1972).

The description of Wyoming big sagebrush as a distinct subspecies (Artemisia tridentata ssp. wyomingensis) by Beetle and Young (1965); the identification of significant root system differences of Wyoming big sagebrush and basin big

sagebrush (A. t. ssp. tridentata) by Nichols (1964); and the differential water acquisition ability of sagebrush from that of herbaceous species (Fisser 1968) provided the information that Wyoming rangeland yield was closely related to sagebrush dynamics as well as environmental criteria.

Hyder and Sneva (1962), at the Squaw Buttes research station in Oregon, were among early researchers to study chemical control of big sagebrush. They recognized that abundance and yield of this shrub was highly variable. Climate and site characteristics were noted as being extremely influential to growth of this shrub as well as to its rate of development.

DESCRIPTION OF STUDY AREAS

Location, Climate, and Soils

Intensive studies of plant phenology were initiated in 1973 on 12 locations in western Wyoming (fig. 1). These locations represent the Big Horn Basin, the Wind River Basin, the Little Colorado Desert, and Bear River drainages. The sites were all on sagebrush-dominated rangelands identified in general as semiarid. The areas of study express a broad ecological amplitude. The 12 research locations encompass the majority of western Wyoming, some 200 miles (325 km) from north to south and 225 miles (365 km) from east to west, an area of some 45,000 mi² (120 000 km²). Elevation range is 2,300 feet (700 m), from 4,920 to 7,220 feet (1 500 to 2 200 m)(Kleinman 1976).

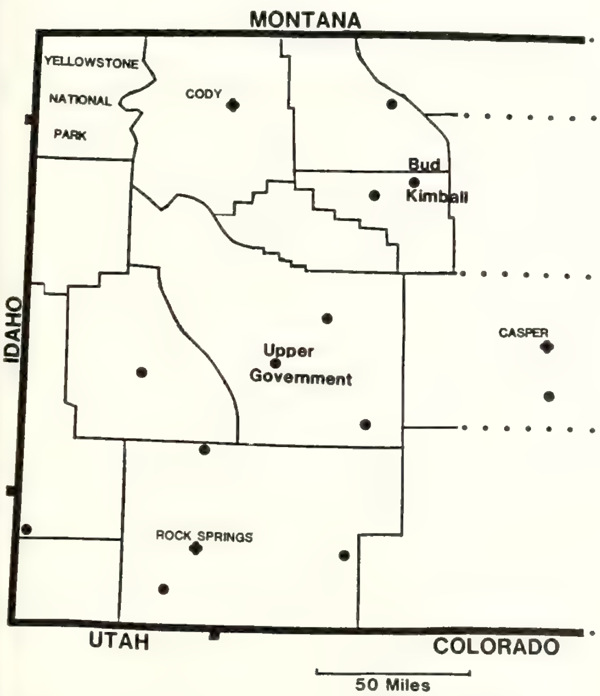

Figure 1.--Map of central and western Wyoming showing geographic distribution of 12 intensive phenology research locations(represented by the black dots.

Average annual precipitation is 8.7 inches (220 mm). Values are as low as 6.7 inches (170 mm) and as great as 11.0 inches (280 mm), a range of 4.3 inches (110 mm). Approximately three quarters of all precipitation occurs during winter and spring. The remainder is almost equally distributed during summer and fall.

Range of mean annual temperatures among sites is 12 °F (7.0 °C), from 35 to 47 °F (1.4 to 8.5 °C). Approximately 100 days are frost free. Mean seasonal temperatures range from 48 to 57 °F (9 to 14 °C) in the spring, and from 57 to 73 °F (9 to 14 °C) in the summer. Summer and winter temperatures often exceed 100 °F (38 °C) and -20 °F (-29 °C), respectively, and extremes of 110 °F (38 °C) and -50 °F (-45 °C) have been recorded (Kinucan 1983).

Soils are of two orders--Aridisol and Entisol. Diagnostic horizons are characterized by calcic and argilic components, and pH is moderately alkaline (Young and Fisser 1979).

Vegetation and Animals

In addition to big sagebrush, the dominant at all locations, associated woody species include black sagebrush (Artemisia nova), Douglas and rubber rabbitbrush (Chrysothamnus viscidiflorus and C. nauseosus), winterfat (Ceratoides lanata), broom snakeweed (Gutierrezia sarothrae), and occasionally gray horsebrush (Tetradymia canescens), spiny hopsage (Grayia spinosa), Utah juniper (Juniperus osteosperma), true mountain mahogany (Cercocarpus montanus), and western serviceberry (Amelanchier alnifolia). Kuchler (1964) identified the areas as sagebrush steppe and wheatgrass-needlegrass-shrub steppe zones.

The prevalent grass is western wheatgrass (Agropyron smithii). Other common genera are Poa, Koeleria, Oryzopsis, Stipa, and Sitanion. The annual cheatgrass brome (Bromus tectorum) was seldom present, reflecting the nonMediterranean climate of the region.

Forage utilization occurs primarily from cattle and sheep. Abundant pronghorn antelope (Antelocapra americana), mule deer (Odocoileus hemionus), feral horses (Equus caballus), and a variety of small mammal, reptile, and avian species are present.

METHODS

Plant phenology for all species was identified by developmental phases (table 1). Numerical scores were assigned from 1.0 to 8.0 for description of vegetative development and from 9.0 to 18.0 for reproductive development (Hargis 1980). Each phase was further subdivided at the decimal level (Fisser and Hargis 1982). These described visually apparent vegetal changes and reproductive development, when present. All flowering species at each study area were included in the inventory.

Table 1.--Numerical scoring values for vegetative and reproductive phenophases of big sagebrush developed during the 10-year intensive phenological research program in Wyoming

Score	Phenophase description
1.0	Winter dormancy
2.0	Vegetation bud development
3.0	New leaf development
4.0	Twig elongation
5.0	Twig elongation completed
6.0	Vegetative parts browning
7.0	Fall leaf - shed and/or regreening
8.0	Winter dormancy (revert to 1.0)
9.0	Floral bud development recognizable
10.0	Bloom initiation to 10 percent bloom
11.0	Midbloom - 10 to 25 percent bloom
12.0	Late bloom to seed formation
13.0	Seeds in milk stage
14.0	Seeds in dough stage
15.0	Seeds maturing
16.0	Seed cast - floral parts browning
17.0	Fall reproductive regreening
18.0	Winter dormancy (revert to 8.0)

Phenological observations were made at approximately 14-day intervals through the April to September growing season. At each location 20 individual sagebrush plants were identified along a permanent 100- foot (30-m) tape by coordinate distances at 5-foot (1.5-m) intervals. Cumulative precipitation, maximum and minimum air temperature, soil moisture, and soil temperature were obtained concurrently at each location (Fisser and Kleinman 1974; Kleinman 1976).

ANALYSES

Temporal phenological scores were combined by species, sites, and years. These arrays exhibited broad variability, as would be expected. Phenological sample adequacy was approached with a slight modification to the common test

$$n = \frac{t^2 s^2}{e^2}$$

with e set at $\pm$ 0.2 phenophase (Kinucan and Fisser 1984). A nonlinear growth form model was used to quantify phenologic patterns among species and among species groups of differing life-forms, both within and among sites (Ralston 1981; Kinucan 1983).

For this report, the phenological data of big sagebrush at two sites, the Bud Kimball in the Big Horn Basin and the Upper Government over 100 miles (160 km) distant in the Wind River Basin, are presented (fig. 1). A test of paired means by site over years was used to derive indication of similarities and differences. Detailed analyses combined for all 12 sites have been presented (Fisser and others 1983; Kinucan 1983; Kinucan and Fisser 1984).

RESULTS

The phenological records of big sagebrush at the Bud Kimball (BK) and Upper Government (UG) sites are graphically displayed in figure 2. At BK early spring warmup in 1982 caused early expression of new vegetative development, but later cool temperatures and moderate growing season precipitation caused normal progression through the leaf and stem phenophases. Adequate moisture and moderate later summer temperatures maintained an almost linear vegetative phenologic development rate. The early growth initiation wa[s] also reflected by earlier than normal floral bud manifestation. Optimum weather conditions during summer and fall caused slow reproductive development.

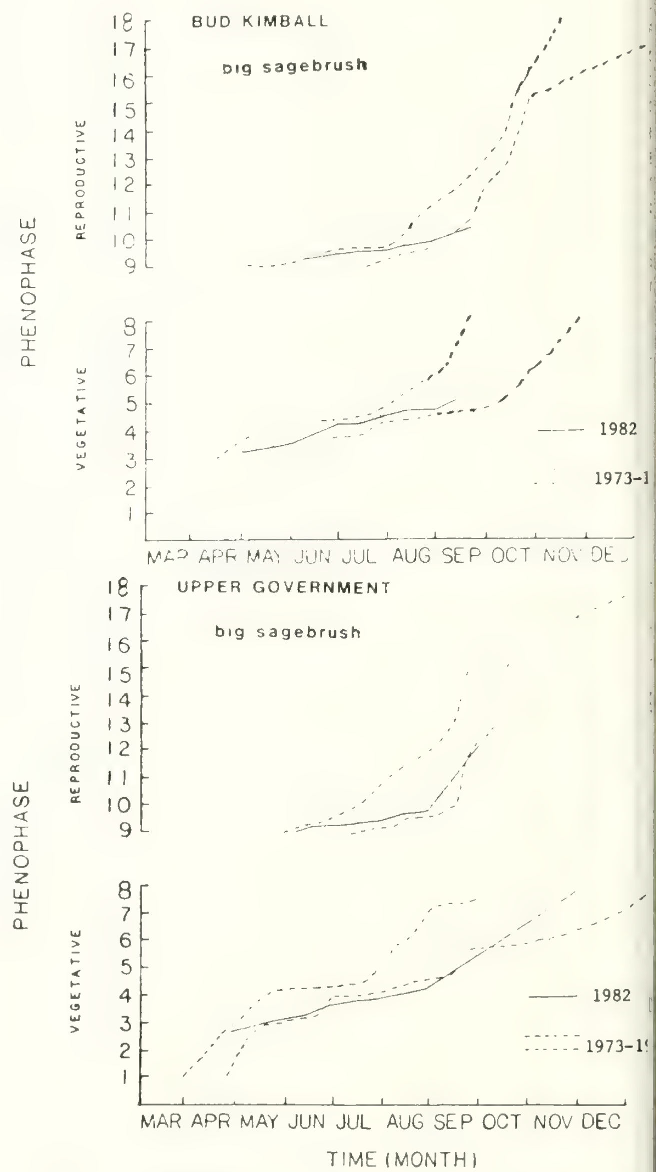

Figure 2.--Ranges of vegetative and reproductive phenological development of big sagebrush at the Bud Kimball (upper) and Upper Government (lower) research locations. Climatic variability during the 10th year of study (1982) caused such slow development that phenological values exceeded the limits of the previous 9 years.

At UG, vegetative growth development in 1982 also initiated early. Atypically cool spring temperatures and good moisture, however, maintained a slower rate of development than normal for the summer months. As a result, vegetative phenology exceeded the bounds set during the first 9 years during the midsummer growing period. Reduced fall moisture availability increased the vegetative phenologic progression rate so that maturation occurred near normal time. Big sagebrush reproductive expression at UG was early also, and the development rate was slower than during 1973 to 1981, until increased progression occurred during the fall.

The lower elevation (1 430 m), warmer temperatures, and commonly less winter snow cover at BK compared to UG (1 805 m) contributes to its earlier growth expression. The more moderate late spring-summer temperatures at UG, however, contribute to a slower vegetative phenologic progression rate than at BK (table 2). The slower development rate generally contributes to enhanced sagebrush herbage yield. The 29-day longer period noted for mean vegetative phenological development at UG was obviously in response to greater late fall soil moisture availability than at BK. Reproductive phenophase was initiated earliest at BK, but UG was generally more advanced during the later growing season. The higher elevation of the latter site reduced the reproductive phenophase time to 164 days compared to 186 at BK.

Table 2.--Julian dates of phenophase attainment at the Bud Kimball (BK) and Upper Government (UG) sites and mean days of difference of UG from BK for the 10-year mean records from 1973 through 1982

Phenophases	Julian dates		Days of difference
Vegetative	BK	UG	
1.0	108	104	4
2.0	116	113	3
3.0	128	135	-7
4.0	163	175	-12
5.0	248	235	13
6.0	267	266	1
7.0	290	293	-3
8.0	305	330	-25
(1-8)	(197)	(226)	(-29)
Reproductive			
9.0	162	171	-9
10.0	233	228	5
11.0	247	238	9
12.0	265	255	10
13.0	277	267	10
14.0	289	277	11
15.0	294	289	5
16.0	305	298	7
17.0	327	308	19
18.0	348	335	13
(9-18)	(186)	(164)	(22)

Environmental constraints resulted in a short growing season during which plant development was quite active unless limited by extreme temperature or drought. Cold spring temperatures generally suppressed rate of early development. Midsummer drought and warm temperatures caused an increased maturation rate and initiated senescence. The shrubs were influenced by early season, cool temperatures; however, late season development was curtailed little by surface moisture unavailability. Deep-rooted woody plants were able to utilize water from 1 to 5 feet (0.3 to 1.3 m) below the surface at depths not available to the roots of most herbaceous species.

These two sites were not at the complete extremes when compared to the other 10 locations. They do, however, represent diverse environmental characteristics rather easily explainable in terms of precipitation and temperature differences.

Those that received the least annual precipitation received the greatest proportion during winter and spring. Differences in effective moisture among sites thus were minimal because the dominant cool season species were able to efficiently utilize spring precipitation (Kinucan and Fisser 1984).

Mean annual temperature differences among sites had little effect on phenological development rates. The only significant thermally related differences in mean phenological development among species or growth forms, among sites, occurred when mean annual temperatures differed by at least 9 °F (5 °C). Soil temperature was one of the major primary driving factors that affected rate of phenological development. Significant changes in plant growth occurred with as little as 1 °F (0.5 °C) change in soil temperature. Relationships between soil moisture and phenological development rate were less obvious (Kinucan 1983).

Other environmental phenomena that were quite important in driving and regulating plant growth were: precipitation from fall through spring, soil moisture at various depths, and maximum and minimum air temperatures. Field data interpretation was based on multiple regression and step-wise selection analysis procedures. These were used to substantiate or reject hypotheses relating to comparative similarity, phenological information, and 15 environmental variables (Kinucan and Fisser).

Within sites, vegetative phenodynamics of species within growth forms such as big and black sagebrush exhibited significant similarity throughout the growing sequence ($p \leq 0.01$). Seven perennial grasses expressed group similarity patterns ($p \leq 0.01$): Sandberg bluegrass (Poa secunda), bottlebrush squirreltail (Sitanion hystrix), bluebunch wheatgrass (Agropyron spicatum), western wheatgrass (A. smithii), needleandthread (Stipa comata), Indian ricegrass (Oryzopsis hymenoides), and junegrass (Koeleria cristata). Although not statistically different, they of course, did not develop identically (Young and Fisser 1979). The sequence of development, from most rapid to slowest, generally occurred in the order as listed.

Significant similarity among growth forms was noted only for the perennial forbs, such as scarlet globemallow (Sphaeralcea coccinea) and low fleabane (Erigeron pumilus), that developed synchronously with the grass species. Phenological patterns of annuals were highly variable and quite sensitive to environmental factors that prevented long-term patterns from forming.

The patterns of phenological development that were consistent and repeated among sites were (1) early and rapid perennial grass development, (2) closely following development of perennial forbs, and (3) later development of shrubs with the most protracted sequence of phenological phases.

Developmental differences noted among growth forms can, in part, be attributed to differential partitioning of limited water resources once cold spring temperatures were no longer a limiting factor (Hughes 1977). Soil moisture at shallow depths and to 24 inches (60 cm) was depleted by late June or early July (Fisser 1968). At that time the grass species reached vegetative maturity. The forbs, which developed more slowly early in the season, generally began senescing by late June. Although there were noticeable variations in phenologic progression for portions of the season, there were no statistically significant differences in season-long development. At some sites, development started late in the season due to cold temperatures. Even with a late start, however, most herbaceous plant species at all sites reached maturity and senesced at the same time as at the other sites where spring growth initiation may have been as much as 40 days earlier.

This "catching up" of development demonstrates a vegetative phenophase condensation phenomenon. This, in essence, is a compression of the entire sequence of development into a shorter than normal time period. Reproductive phenology is not nearly as flexible and, as noted earlier, at these latitudes and elevations, may not even be initiated because of environmental stresses.

Within semiarid rangeland communities of Wyoming, various groups of species exist that express similar patterns of phenological development. These phenologically similar groups tend to be found among species with similar growth forms and rooting habits. Phenological similarities within group forms can be attributed to likenesses in moisture acquisition and cold temperature avoidance, in part controlled by similar morphological features. Conversely, differences among growth forms may be explained by these same attributes.

Within growth-form groups, variation was also minimized as a result of a vegetative phenophase condensation phenomenon. Although this phenomenon also occurred between growth forms, significant differences ($p \leq 0.01$) were evident, demonstrating a true difference in growth form strategies and niche specialization. Observations of the unique cumulative patterns of vegetal development expressed by growth forms led to speculation tha adaptations to water and temperature stress are functions of growth form, which, in turn, dictat phenologic expression.

SUMMARY

A numerical scoring system was used to monitor vegetative phenodynamics independently of reproductive development. Many plant species of semiarid regions produce flowers and seeds inconsistently from year to year. The complete sequence of annual herbage growth response to climatic and environmental conditions usually progresses from spring bud initiation through le maturation during summer and fall. Sometimes extreme climatic stress can actually force early spring or summer dormancy and senescence of even the vegetative growth. A numerical quantificati of plant growth phases can be used to better identify the plant response relationship to environmental driving variables

This study was conducted at 12 diverse semiarid sagebrush locations in Wyoming from 1973 through 1982. Intensive study of big and black sagebrus and western and bluebunch wheatgrass involved 20 plants of each species, at each location, which were monitored at 2- to 3-week intervals during the growing season. Permanent transect lines we installed to simplify relocation of each plant. Phenology of the four prime species was monitore to identify subphase appearance changes that wer definitive for each. All other plant species we monitored using rather general and classical development phases and with lesser definition of subphase changes.

Big sagebrush phenology from a drier and lower elevation site (BK), and from a more mesic, high elevation site (UG), were presented to show dissimilarities and likenesses of annual vegetative development. Intrinsic site differences that modified the rate of phenologic progression were apparent. Occasional weather extremes, at any location, caused development ra changes that superceded the inherent progression dynamics expected at a site.

Precipitation, seasonal air temperature extremes and soil moisture most directly influenced phenologic progression, as would be expected. Plant species with similar growth forms, and especially similar root structure characteristic exhibited similar phenodynamics. Vegetative phenology was more flexible than reproductive. Ability to extract soil moisture for a longer ti in the fall by the deep-rooted shrubs such as sagebrush was exhibited by later seed maturation as well as a longer leaf development period than grasses and forbs. A perennial grass understory enhanced infiltration which provided long-term moisture availability and a greater competitive ability by the shrubs.

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BIOLOGY AND ECOLOGY OF SAGEBRUSH IN WYOMING: IV.

VALIDATION OF A RANGELAND PRODUCTION MODEL (ERHYM) FOR SAGEBRUSH SITES

J. Ross Wight, Herbert G. Fisser and Clayton L. Hanson

ABSTRACT: A rangeland model (ERHYM) was tested with long-term herbage yield records (1965-82) from two sagebrush-grass range sites in central Wyoming. Soil water and soil temperature data for 1963 to 1968 from one of the sites were used to validate the model's soil water balance and soil temperature components. The model accounted for about 50 percent of the variation in the field-measured total yields for the two sites. There was good agreement between the model-predicted and field-measured soil water and soil temperature.

INTRODUCTION

ERHYM (Ekalaka Rangeland Hydrology and Yield Model) is a climate, water-balance model initially developed to predict herbage yields as a function of climate (Wight and Neff 1983). Since its initial development, ERHYM has undergone a series of modifications and improvements. A runoff routine from the CREAMS model (Knisel 1980) that is based on the SCS curve number procedure, a soil temperature simulation routine from the EPIC model (Williams and others 1983), and a climate generating routine from the SPUR model (Wight 1983) have been added to enhance its accuracy and utility. ERHYM is a physically based, process-oriented model and should function effectively when the state variables and model parameters are properly quantified. It has a wide range of potential applications as a tool for researching and managing the rangeland ecosystem.

ERHYM was initially developed and validated for a mixed grass prairie ecosystem (Wight and Hanks 1981). It was successfully applied to a sagebrush-grass range site in southeastern Montana (Wight and Neff 1983). Some preliminary testing of ERHYM's water-balance and soil temperature routines was accomplished using data from sagebrush-grass range sites in southwestern Idaho (Wight and others 1983; Wight 1984). The availability of long-term precipitation and herbage production records for the Wind River Basin region of central Wyoming provided the opportunity to test and validate ERHYM on sagebrush-grass range sites in another geographical region (Fisser, these proceedings).

PROCEDURE

Site Description

Yield and climatic data from two sagebrush-grass range sites in the Wind River Basin of central Wyoming were used in this study. Soils at both sites are classified as fine, loamy, mixed soils of the Aridisol order. Big sagebrush (Artemisia tridentata) is the dominant cover and western wheatgrass (Agropyron smithii), mutton bluegrass (Poa fenderiana), and sandberg bluegrass (P. sandbergii) account for most of the forage production on both sites. Site elevation and average annual precipitation are 7,106 feet (2 166 m) and 9.88 inches (25.1 cm), respectively, for the Granite Mountain site and 6,230 feet (1 899 m) and 9.33 inches (23.7 cm), respectively, for the McGraw Flats site. Herbage dynamics for the study period are shown in table 1.

Climatic Data

Precipitation was collected in simple aluminum raingauges installed at the exclosure of each study site. The raingauges had a diameter of 2.79 inches (7.09 cm) so that each 100 mL of water collected in the gauges was equivalent to 1.0 inch (2.54 cm) of precipitation. Oil was added to the gauges to prevent evaporation, and antifreeze was added during the winter months to prevent freezing. Precipitation was recorded four times each year: April 15, July 1, September 1, and October 15.

A daily precipitation record was developed for each study site by prorating the site precipitation records with nearby U.S. Weather Bureau stations using a reciprocal distance squared method such as the one by Wei and McGuinness (1973). Daily precipitation records obtained in this manner are generally satisfactory for predicting herbage production, but may induce a few day-to-day discrepancies between simulated and field-measured soil water content values. Daily solar radiation obtained from the climate-generating routine of the model and air temperatures from the U.S. Weather Bureau statio

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Table 1.--Dynamics of field-measured and model-predicted herbage yields for Granite Mountain and McGraw Flats

	Sample size	Mean yield	Range	Standard deviation
	Years	Lb/acre[1]		
Field-measured				
Granite Mountain				
Grasses and forbs	16	263	186-404	61
Shrubs	10	196	91-363	93
Total	10	460	299-633	118
McGraw Flats				
Grasses and forbs	18	238	82-370	84
Shrubs	12	223	0-382	110
Total	12	462	82-680	174
Model-predicted				
Granite Mountain				
Grasses and forbs	16	263	184-300	29
Total	10	460	322-593	85
McGraw Flats				
Grasses and forbs	18	237	166-293	56
Total	12	459	235-564	122

[1]Lb/acre x 1.12 = kg/ha.

at Lander, WY, were used for most of the simulations. The model was also run using "generated" maximum and minimum air temperatures.

Soil water content and soil temperature were measured at the Granite Mountain site periodically during the summer months of 1963, 1965, 1967, and 1968. Soil water was measured by the neutron scatter method at soil depths of 6, 12, 18, 24, 36, 48, and 60 inches (15, 30, 46, 61, 91, 122, and 152 cm). Soil temperatures were measured at depths of 1, 8, 15, and 22 inches (2.5, 20.3, 38.1, and 55.9 cm).

Herbage Yield Data

Herbage yields were determined both inside and outside an exclosure at each study site by clipping the herbaceous vegetation by species at ground or crown level from 20 1- by 1-ft (2.5- by 2.5-cm) quadrats spaced systematically along a randomly located 100-ft (30-m) steel tape. Twenty quadrats inside and 20 more outside the exclosure were clipped at each site each year. Annual site yield was determined as the average of all 40 quadrats. The vegetation was clipped within 1 month following peak standing crop. Beginning in 1971, the yield of shrubs and mat-forming species was obtained during late September and October by using a modified double-sampling technique. Weight units were estimated on 20 4- by 5-ft (1.2- by 1.5-m) quadrats inside and 20 quadrats outside the exclosure. Three of the weight units for each species were clipped and weighed to calibrate and check estimations. On areas outside the exclosures, where grazing had occurred prior to clipping, utilization estimates by species were used to adjust the yield estimates. Although herbage yields inside the exclosures were slightly higher than outside, the year by grazing treatments (inside and outside the exclosures) were generally not significant, and so the data from both inside and outside the exclosures were combined to provide a larger sample size.

Model Validation

The effectiveness of ERHYM as a forage yield model depends on its ability to simulate an accurate soil water balance. Because there is little summer runoff from these sites, the soil water-balance component of the model was tested using single growing season runs in which actual field-measured soil water values were used to initialize the model at the beginning of each growing season. Soil water measurements that coincided with the beginning of the growing season were available only in 1963 and 1965. Continuous runs, 1963 to 1967, were utilized to test the model's ability to simulate overwinter recharge. For yield predictions, continuous runs

for 1965 through 1980 for the Granite Mountain study site and 1965 through 1982 for the McGraw Flats study site were used to match the available yield data. In continuous runs, the soil water content variables were not reinitialized at the beginning of each growing season with field-measured soil water data. They were model simulated values carried over from year to year.

The model's ability to simulate soil temperatures was evaluated by comparing model-predicted soil temperatures at the Granite Mountain site with field-measured values for 1963-1968.

RESULTS AND DISCUSSION

Five years of soil temperature measurements on the Granite Mountain site provided data for validating the model's soil temperature routine. Accuracy of model-predicted temperatures (fig. 1; table 2) appears adequate for the needs of the water-balance component for the model. In the model, soil water uptake from the subsurface soil layers is reduced to zero as soil temperature decreases from 63 to 32 °F (17 to 0 °C). Above 63 °F (17 °C) soil temperature has no effect on soil water uptake. While such a temperature constraint is necessary to represent the effects of soil temperature on water uptake, the model is not sensitive to small deviations from actual soil temperature values because most of the evapotranspiration takes place when the soil is relatively warm.

A major test for the model is its ability to simulate soil water content. If the model can accurately simulate the seasonal soil water regime, then the model-calculated yield indices (actual transpiration/potential transpiration) are also assumed to be reasonably accurate. The best test of the water balance component is single growing season simulations where the model can be initialized with actual beginning soil water content values. A comparison of field-measured and model-predicted soil water contents for the Granite Mountain site in 1965 (fig. 2) indicates the model's ability to simulate soil water regimes for a single growing season. Similar results were obtained for 1963.

Simulating continuous soil water regimes over the winter is more difficult. To account for the processes of snow accumulation, snowmelt, and infiltration into frozen or partially frozen soils requires model complexity beyond the scope of ERHYM. In ERHYM, precipitation is accumulated as snow when temperatures are below freezing, and snow is melted by a simple temperature-driven algorithm from CREAMS (Knisel 1980) when air temperatures are above freezing. There are no adjustments of SCS curve numbers to reflect the effects of frozen soil on runoff. Nevertheless, the model-predicted soil water for a 5-year period at Granite Mountain compared reasonably well with field-measured soil water, indicating the model's ability to simulate continuous year-round soil water regimes (fig. 3). Only in 1965 were there major discrepancies at the beginning of the growing season between field-measured and model-predicted values.

Correlation coefficients for field-measured versus model-predicted herbage yields for 1965-80 for Granite Mountain and 1965-82 for McGraw Flats are presented in table 3. The model was better able to predict total yields than the grass-plus-forbs or shrub yields. Yields were based on a calculated actual transpiration/potential transpiration (T/T_p) ratio. The calculated transpiration value represents the total vegetation complex, and it is not partitioned by species; however, where the production of one component, such as sagebrush, is relatively

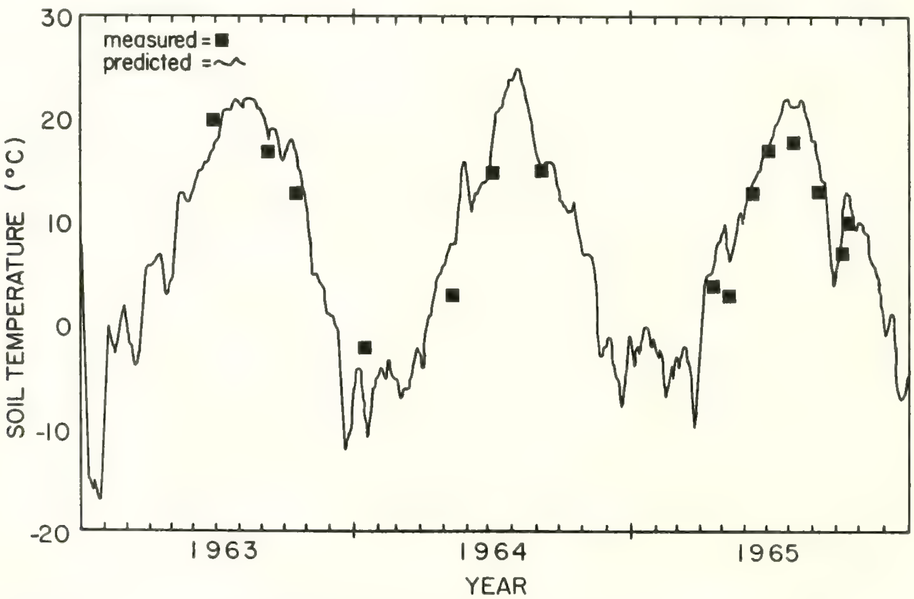

Figure 1.--Comparison of field-measured and model-predicted soil temperatures at the 18-inch soil depth, Granite Mountain, WY.

Table 2.--Correlation between field-measured and model-predicted soil temperatures at the Granite Mountain site

Comparisons	Sample size (n)	Soil depth[2] (inches) 6	12	18	24
		r-value[3]			
Single year simulations[1]					
1965	8	0.90	0.89	0.94	0.94
1967	9	.81	.87	.87	.87
Continuous simulation					
1963-65	27	.76	.83	.89	.88

[1]The model was initialized each year using field-measured soil water content values.

[2]Soil depths of 6, 12, 18, and 24 inches are equivalent to 15, 30, 45, 60 cm.

[3]All correlation coefficients (r) are different from 0.0 at the 0.10 probability level.

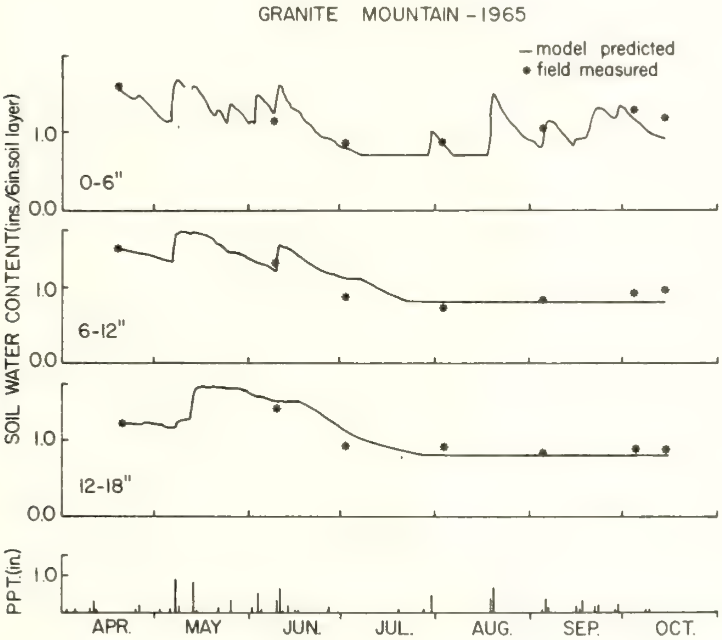

Figure 2.--Comparison of field-measured and model-predicted soil water for a single growing season at the 0-6-, 6-12-, and 12-18-inch (0-15-, 15-30-, 30-45-cm) soil depths.

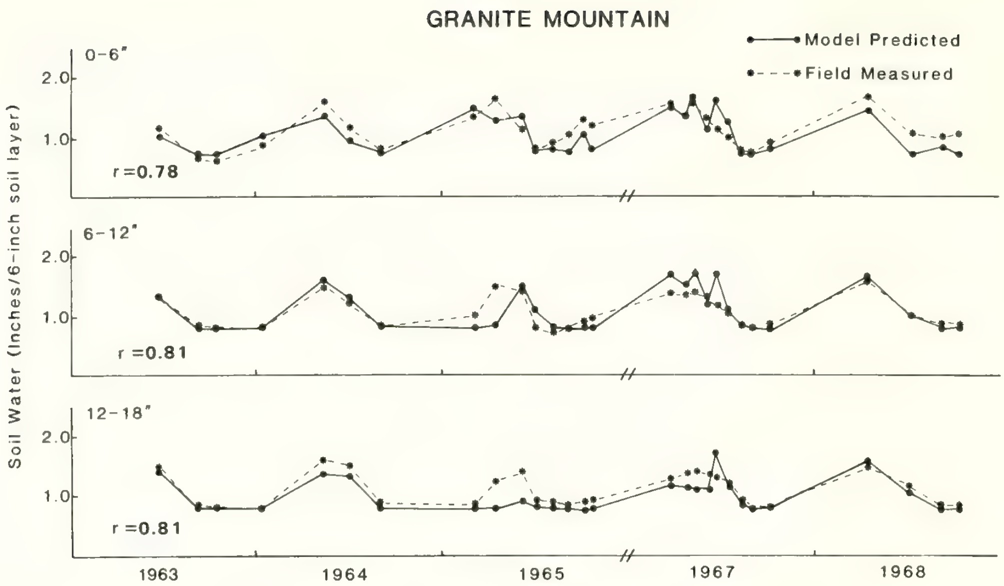

Figure 3.--Comparison of field-measured and model-predicted soil water for the 0-6-, 6-12-, and 12-18-inch (0-15-, 15-30-, and 30-45-cm) soil depths.

Table 3.--Correlation between field-measured and model-predicted herbage yields for 1963-82

Vegetation	Study site			
	Granite Mountain		McGraw Flats	
	Mode 1[1]	Mode 2[2]	Mode 1	Mode 2
	r-value			
Grasses and forbs	[3]0.40a	0.47a	0.68a	0.68a
Shrubs	0.34	0.39	0.49	0.58
Total	0.69a	0.68a	0.72a	0.77a

[1]Mode 1 simulations used actual air temperature values from the U.S. Weather Bureau Station in Lander, WY.

[2]Mode 2 simulations used model-generated air temperature values.

[3]Correlation coefficients followed by "a" are different from 0.0 at the 0.10 probability level.

stable, the model may have utility for predicting annual production of the other components, such as grasses and forbs.

Departures from a 1-to-1 relationship between model-predicted and field-measured values ($r = 1.0$) reflect large yield sampling errors; the model's inability to simulate T and T_p without error; and the lack of a 1-to-1 T/T_p -yield relationship. High sampling errors in the yield data are reflected by average coefficients of variation of 52, 49, and 36 percent for the grasses plus forbs, shrubs, and total yield, respectively, for the two study sites. While sampling variability of this magnitude is common on sagebrush-grass rangelands, the high variability of the actual herbage yield estimates adds to the difficulties of model development and validation.

Variation in annual production as determined from field samples was relatively small, especially in the grasses-plus-forbs component (table 1). On the Granite Mountain site, 75 percent of the annual yield was within a 90 percent sampling confidence interval of the 16-year mean. The correlation coefficient between model-predicted and field-measured grasses plus forbs yield was only 0.47. Yet, 75 percent of the model-predicted yield was within a 90 percent confidence interval of the associated field-measured yield values. For the Granite Mountain grasses-plus-forbs yield, the single long-term mean was as effective for predicting annual yields as the model. For total yield, the yearly variation was much greater. Only about 20 percent of the Granite Mountain and McGraw Flats total annual yields was within a 90 percent sampling confidence interval of the long-term mean yield. Comparison of ranges and standard deviations for the field-measured and model-predicted yields in table 1 indicates that the model represented the total yield dynamics better than that of the forbs plus shrubs.

The use of stochastic-generated air temperatures had very little effect on predicted yields, compared to the use of actual weather station air temperatures (table 3). For long-term simulations, it appears that generated solar radiation and air temperature values are adequate.

SUMMARY

Overall, the ERHYM model performed reasonably well on the two sagebrush range sites in central Wyoming. With better quantification of the state variables and model parameters such as crop coefficient and transpiration coefficient, model accuracy would likely be improved. The results of this study indicate that the ERHYM model has a wide range of potential applications in researching and managing sagebrush-grass rangelands.

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BIOLOGY AND ECOLOGY OF SAGEBRUSH IN WYOMING: V.

HERBAGE YIELD DYNAMICS AND SEASONAL PRECIPITATION RELATIONSHIPS

Clayton L. Hanson, Herbert G. Fisser, and J. Ross Wight

ABSTRACT: We investigated the linear relationship between seasonal precipitation and total herbage production at seven rangeland sites in central Wyoming. Total winter-plus-spring precipitation was the best herbage yield indicator where, on the average, 1 inch of precipitation produced 58 pounds of ovendry material. We also found that the coefficients in the herbage yield-crop year precipitation model proposed by Sneva and Hyder (1962b) and Sneva and Britton (1983) were different from the coefficients that gave the best linear relationship based on site data from central Wyoming.

INTRODUCTION

In many studies, simple or multiple linear regression analyses, using herbage yield as the dependent variable and seasonal precipitation as the independent variable, have been used to develop predictive equations. However, attempts to correlate annual herbage yields of semiarid rangelands with annual precipitation have generally been unsuccessful. This is due primarily to the variable distribution of precipitation and to the fact that range plants generally have the greatest rate of growth during the spring and early summer and little, if any, growth during fall and early winter. Use of seasonal or combinations of monthly precipitation have helped account for the distribution effects and, in many situations, have provided reasonably accurate herbage yield estimates. In Canada, Smoliak (1956) found that May and June precipitation provided good estimates of yield ($r = 0.86$). In North Dakota, Rogler and Haas (1947) correlated April-July precipitation with annual herbage yields ($r = 0.76$). Also in the Northern Great Plains, Power and Alessi (1970) and Wight (1978) found that May was the best single month to index annual herbage production. Sneva and Hyder (1962a) reviewed studies in the intermountain region which indicated that winter and spring precipitation were closely correlated with annual herbage production.

Precipitation-herbage yield relationships developed through regression techniques tend to be site specific. To overcome this dependency, Sneva and Hyder (1962b) and Sneva and Britton (1983) expressed herbage yield and "crop-year" precipitation as ratios of long-term medians.

In this study, we investigated the linear relationships between seasonal precipitation and total herbage yield at seven sites in central Wyoming where precipitation and yield records were available from 1971 through 1982 (Fisser, these proceedings). We also used the same data set to develop a yield-precipitation index model as proposed by Sneva and Hyder (1962b) and Sneva and Britton (1983) for herbage yield adjusting and forecasting. They found that one set of parameters could be used to represent the intermountain region and we wanted to know if their parameter values could be used outside the intermountain region.

METHODS

Site Description

The seven central Wyoming study sites were located in the Wind River Basin, which is both a structural and drainage basin. Its northern boundaries contact the southern portions of the Owl Creek and Big Horn Mountains. The Wind River Range forms the west and southwesterly boundaries, while the southeast and eastern limits are the Sweetwater Escarpment and the Rattlesnake Mountains. The basin is asymetrical in shape with lowest elevations near the Owl Creek Mountains. Elevations range from 4,000 to 7,200 feet (1 219-2 195 m).

The Wind River Basin has a semiarid climate. At Riverton, mean annual precipitation is 8.54 inches (21.7 cm) and mean annual temperature is 43.2 °F (6 °C). The seven central Wyoming sites used in this study are listed in table 1. Site elevation ranged from 5,220 feet (1 591 m) at the Shoshoni #7 location to 7,100 feet (2 164 m) at the Granite Mountain area. Annual precipitation varied from 8.09 inches (20.5 cm) at Shoshoni #7 to almost 10.00 inches (25.4 cm) at Lower Government.

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Table 1.--Annual and seasonal precipitation and herbage yield for seven study sites in central Wyoming

Site	Elevation	Slope	Aspect of slope	Average precipitation: Annual[2]	Average precipitation: Winter-spring[3] season	Average herbage yield[1]: Inside	Average herbage yield[1]: Outside	Average herbage yield[1]: Means of inside and outside
	Feet	Percent	Degrees	-------Inches-------		-------Lb, ovendry weight-------		
Sweetwater	6150	3.0	145	8.88	6.33	460	436	448
McGraw Flat	6650	1.0	63	9.19	6.31	539	484	512
Granite Mountain	7100	0.5	30	9.03	6.32	524	490	507
Lower Government	5500	0.5	75	9.97	7.52	728	648	688
Upper Government	6080	0.5	90	9.03	7.22	535	422	479
Lander Ant	5350	1.5	143	8.33	6.66	302	325	314
Shoshoni #7	5220	0.5	15	8.09	6.12	326	338	332

[1] Average total herbage yield based on the years used in this study.

[2] Average based on 1960 through 1982 record.

[3] Average based on 1971 through 1982 record.

Soils were Aridisols, including mixed, typic, and frigid Haplargids. They exhibited moderate percolation, were well drained, of moderate alkalinity, and contained a zone of increased effervescence ($CaCO_3$) in the lower "B" horizon. Sand and clay content was variable and the textural class was loamy. The "A" horizon was usually about 3 inches (7.6 cm) thick and the "B" horizon about 15 inches (38.1 cm) thick.

PROCEDURES

Herbage production was obtained in an exclosure and adjacent grazed area at each site. Production was determined by clipping herbaceous species at ground or crown level. Clipping was conducted on or near the same date each year at each study site. Production sampling was initiated each year shortly after July 4 beginning on sites dominated by Gardner saltbush (Atriplex gardneri), which was treated as an herbaceous species. All new annual growth was clipped at that time for determination of total production. Clipping was completed by August 22 each year. Clippings were ovendried at 158 °F (70 °C) for 24 hours prior to weighing.

On areas where animal use had occurred prior to clipping, estimates of utilization were made by species. These estimates were made at the time each plot was clipped. Utilization values were averaged by species for 20 plots and used to adjust production for herbage lost by herbivory. Calculated production estimates given in table 1 were corrected for utilization and represent total production.

An estimate of total production was derived for each site by adding the shrubby and mat-forming species production to the clipped production.

Shrub, mat-forming, and pricklypear herbage production was obtained using a modified double-sampling technique during September and October. Weight units were estimated on 20 randomly located macroquadrats, 4 ft by 5 ft (1.2 m by 1.5 m), subdivided into 6-inch (15.2-cm) squares. Macroquadrats were 6-12 steps apart across the study area.

Shrubby species larger than 36 square inches, primarily big sagebrush (Artemisia tridentata Nutt.), were estimated using the 6-inch square as one weight unit. Mat-forming plants and shrubs smaller than 6 square inches were estimated by weight units of characteristic plant shape and size. Three of the weight units for each species were clipped for weight determination. Each sample was dried in an oven at 158 °F (70 °C) for 96 hours. The average weight in grams for the three weight units, multiplied by the total number of estimated units in 20 quadrats, was converted to pounds per acre as an estimate of annual production. At the same time clipped production data were collected during July and August, pictures of the transects were taken to give a pictorial history from year to year at each study location.

Precipitation data were recorded using metal raingauges installed at each exclosure. The raingauges were constructed with a diameter of 2.79 inches (7.09 cm) so that each 100 mL of water recorded in the gauge was equal to 1.0 inch (2.54 cm) of precipitation. Oil was added to each gauge after reading to prevent evaporation. During the winter months antifreeze was added in known amounts to prevent the gauges from freezing and breaking. Precipitation data were collected four times a year: April 15, July 1, September 1, and October 15.

Regression procedures were used to determine the relationships between annual and seasonal precipitation and total herbage yield by site where the precipitation periods were: (1) fall, September 1 through October 15; (2) winter, October 16 through April 15; (3) spring, April 16 through June 30; and (4) summer, July 1 through August 31. The relationships between seasonal precipitation and the herbage yield from inside and outside the exclosures, and the average of the yield from inside and outside the exclosures were investigated. For the final analyses, the annual yields from inside and outside the exclosures were used as separate samples.

Total winter and spring precipitation by site was used to develop the precipitation indices in the Sneva and Hyder model. Herbage yield indices were developed at each site by using the yields inside and outside the exclosures as separate samples.

DISCUSSION

Regression analyses were used to determine which precipitation season or combination of seasons was the best herbage yield predictor. Initial analyses showed that the winter-spring season gave the best overall prediction results. These analyses also suggested that using the herbage yields from inside and outside the exclosures as separate samples gave the most consistent results. Table 2 is a summary of the regression equations computed from the seasonal precipitation and herbage production at each of the seven study sites.

The slopes of the regression lines varied from 52 to 64/lb/acre (58 to 72 kg/ha) of herbage per inch of precipitation with a mean value of 58, which indicated that 1 inch of winter-spring precipitation produced about 58 lb (26 kg) of herbage (table 2). This was among the lower values Sneva and Hyder (1962a) found for the intermountain area; their values ranged from 33 to 132 lb of herbage/inch (6 to 23 kg/cm) of precipitation. Rogler and Haas (1947) reported about 74 lb/inch (13 kg/cm) of seasonal precipitation for central North Dakota. Smoliak (1956) found that 1 inch of spring and summer precipitation would produce 78 lb (35 kg) at the Manyberries Range Experimental Farm in southeastern Alberta.

Correlation coefficients (r) were significantly different from zero at the 0.01 level, which indicated that there was a linear relationship between seasonal precipitation and total herbage yield. However, the r^2 values for Lower Government and Shoshoni #7 were 0.44 and 0.34, respectively, which reduced the usefulness of the equations developed for these two sites. The 1974 herbage yields were not used in the final analyses of the Lower Government, Upper Government, and Shoshoni #7 sites because herbage yields were so much greater than the measured precipitation would indicate that using the 1974 data would have prevented developing useful prediction equations. The apparent reason for this discrepancy was that the previous fall precipitation was between 4 and 5 inches (10.2 and 12.7 cm). There was only 1 year in the data series when this was the case, so no conclusions could be made about the effect of large fall precipitation amounts on herbage yields at these sites or the other four sites in this study.

The 1976 data were not used for the Granite Mountain, Lower Government, and Upper Government sites because yields were very low relative to the available precipitation, and, again, would have prevented us from developing useful prediction equations. It is not known if the low

Table 2.--Summary of regression analyses of seasonal precipitation (X) vs. total herbage production (Y) from both the exclosure and grazed area at each study site

	Regression equation $Y = a + bX$			Correlation coefficient[1]
Site	a	b	n[2]	r
Sweetwater	88	57	24	0.73
McGraw Flat	108	64	24	.81
Granite Mountain	111	63	22	.82
Lower Government	249	58	20	.66
Upper Government	66	57	20	.74
Lander Ant	-35	52	24	.82
Shoshoni #7	0	54	22	.58

[1] All correlation coefficients are significantly different from zero at the 0.01 level.

[2] Annual herbage yields from inside and outside the exclosures were separate samples (n = number of years x 2).

ields were due to sampling or other conditions uch as seasonal climatological variations.

neva-Hyder Index Procedure

he same winter-spring precipitation and herbage ield data sets used for the final regression nalyses were used to develop herbage forecasting quations based on the Sneva-Hyder procedure Sneva and Hyder 1962b; Sneva and Britton 1983). esults are summarized in table 3. As shown in able 3, the slope varied from 0.63 at Lower overnment to 1.10 at Shoshoni #7, with a mean alue of 0.87 when all site data were grouped. he correlation coefficients (r) were all ignificantly different from zero, which ndicated that there was a linear relationship etween the precipitation index and herbage yield ndex, as with the other regression analyses. The r^2 values were below 50 percent for the Lower Government and Shoshoni #7 sites.

The single regression equation obtained for the seven sites was:

$$Y = 0.87X + 16 \quad (r = 0.71) \qquad (1)$$

where Y is the yield index (percent of median value x 100) and X is precipitation index (percent of median value x 100). Both the slope and intercept of equation (1) were significantly different from the equation proposed by Sneva and Britton (1983). Their equation was:

$$Y = 1.23X - 23 \quad (r = 0.83) \qquad (2)$$

This suggested that the herbage yield-precipitation relationship in the Wind River Basin of Wyoming was different from that of the sample areas used by Sneva and Britton. The crop-year precipitation (September 1-June 30) used by Sneva and Britton was about the same as the season used in this study, so other factors, such as soils and climatic regime contributed to the discrepancy between the two equations. Hanson and others (1983) found that the Sneva-Hyder (1962b) equation represented conditions at the low-elevation areas on the Reynolds Creek Experimental Watershed in southwest Idaho; this also suggested that the precipitation-herbage yield relationships were different between the intermountain region and the Wind River Basin.

The results of this study indicated that the precipitation-herbage yield index procedures proposed by Sneva and Hyder were good procedures for forecasting herbage yield. However, study results suggested that the coefficients in the equation were different for different areas of the country and, therefore, coefficient values must be computed for other areas than the intermountain region.

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Table 3.--Summary of regression analyses of seasonal precipitation (X) vs. total herbage yield (Y) where Y and X are expressed in percent of the median value[1]

	Regression equation Y = a + bX			Correlation coefficient[2]
Site	a	b	n[3]	r
Sweetwater	20	0.80	24	0.73
McGraw Flat	24	.92	24	.83
Granite Mountain	22	.78	22	.83
Lower Government	37	.63	20	.70
Upper Government	12	.89	20	.83
Lander Ant	-11	1.05	24	.83
Shoshoni #7	0	1.10	22	.58
All sites	16	.87	156	.71

[1] See Sneva and Britton (1983).

[2] All correlation coefficients are significantly different from zero at the 0.01 level.

[3] Annual herbage yields from inside and outside the exclosures were separate samples (n = number of years x 2).

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Section 7. Physiology and Growth

PHOTOSYNTHESIS, GROWTH, TRANSPIRATION, AND ^{13}C RELATIONSHIPS AMONG THREE SUBSPECIES OF BIG SAGEBRUSH (ARTEMISIA TRIDENTATA NUTT.)

Carolyn T. Frank, Bruce N. Smith, and Bruce L. Welch

ABSTRACT: Twenty-one accessions of three subspecies of big sagebrush (Artemisia tridentata ssp. tridentata, ssp. wyomingensis, and ssp. vaseyana) were grown in a uniform garden to test the relationship between $\delta^{13}C$ values and photosynthetic efficiency. Individual plants were measured for rates of photosynthesis, transpiration, growth, and $\delta^{13}C$ values. As growth rates increased, so did $\delta^{13}C$ values. Increase in growth indicated an increase in photosynthetic efficiency (CO_2 uptake/H_2O loss). Differences in $\delta^{13}C$ values among subspecies correlated with photosynthetic adaptations to different environmental conditions.

INTRODUCTION

Most plants fix carbon initially into 3-phosphoglyeric acid and are termed C_3 plants (Winter and others 1982). Among other characteristics, these plants exhibit a characteristic range of isotopic discrimination values for the naturally occurring, stable isotopes of carbon. Isotopic values reflect either environmental influences (Smith and others 1976; Vogel 1980) or genetically determined differences in diffusional or enzymatic fractionation (Park and Epstein 1960).

Artemisia tridentata (big sagebrush) is widespread throughout the Intermountain West and varies in size, growth rate, palatability, digestibility, and chemical composition (Welch and McArthur 1979; Welch and Pederson 1981; McArthur and Welch 1982). This paper examines $\delta^{13}C$ values for 21 accessions of A. tridentata grown at a common site as an indication of genetic differences in photosynthetic efficiency within this species.

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MATERIALS AND METHODS

Plant material was grown in a garden established by the Forest Service, U.S. Department of Agriculture in Springville, UT. Three subspecies of Artemisia tridentata (Nutt.), ssp. vaseyana, ssp. wyomingensis, and ssp. tridentata, were collected from 21 accessions throughout the Intermountain West, the majority from Utah. Of the 21 accessions, 10 were A. t. ssp. vaseyana, seven were A. t. ssp. tridentata, and four were A. t. ssp. wyomingensis. Each accession was represented by 1[illegible] plants. The resulting 210 plants were planted at random on a 3- by 3-m grid. Table 1 lists the locations of seed collection sites. Growth rates were determined by measuring the annual length of 15 leaders per plant. Leader lengths were measured from the terminal leaf bud scars to the tip of the current terminal leaves. Leaders were selected at random over the entire crown of the plant. The 15 measurements were pooled together to calculate a plant mean.

The rate of photosynthesis for each plant was determined using the CO_2 depletion method described by Ehleringer and Cook (1980). We, however, added a probe to determine temperature and relative humidity. Carbon dioxide was measured in an infrared gas analyzer operated in the absolute mode.

Transpiration rates were determined using temperature and relative humidity data collected with the gas samples. Leaf samples from each plant were air dried and then combusted using the sealed tube combustion technique of Sofer (1980). After combustion, plant samples were analyzed on an isotope ratio mass spectrometer. Results were expressed as:

$$\delta^{13}C_{PDB} = \left[\frac{R_{sample}}{R_{standard}} - 1 \right] X\ 1000$$

where R = mass 45/mass 44 of sample or standard.

The current year's growth on 10 different branches of each plant was measured during the last week of October 1981 and 1982.

Regression analyses were used to determine the relationship among $\delta^{13}C$ values, growth rates, transpiration rates, and photosynthetic rates. Standard deviations were calculated from the data obtained in each of these areas. Also, an analysis

able 1.--Collection sites for big sagebrush subspecies used to determine rates of photosynthesis and growth

ubspecies	Accession	County and State	Elevation (m)
aseyana	Colton	Utah, UT	2260
	Sardine Canyon	Cache, UT	1800
	Benmore	Tooele, UT	1900
	Petty Bishop's Log	Sanpete, UT	2380
	Durkee Springs	Sevier, UT	2350
	Clear Creek Canyon	Sevier, UT	2130
	Pinto Canyon	Washington, UT	1850
	Indian Peaks	Beaver, UT	2140
	Hobble Creek	Utah, UT	1500
ridentata	Clear Creek Canyon	Sevier, UT	1720
	Big Brush Creek	Uintah, UT	1830
	Loa	Wayne, UT	2140
	Dove Creek	Dolores, CO	2070
	Evanston	Uinta, WY	2020
	Wingate Mesa	San Juan, UT	2060
	Dog Valley	Juab, UT	1700
yomingensis	Evanston	Uinta, WY	2130
	Kaibab	Coconino, AZ	2340
	Trough Spring	Humboldt, NV	1400
	Milford	Beaver, UT	1540

f variance was conducted to test for significant ifferences among the 20 accessions and subspecies.

ESULTS

rowth rates were related to $\delta^{13}C$ values among ubpsecies (fig. 1). Tridentata with the highest verage growth rate also produced the highest verage $\delta^{13}C$ value (table 2). Wyomingensis had the econd highest growth rate, and its $\delta^{13}C$ value was econd highest. Subspecies vaseyana showed the owest average growth rate and had the lowest $\delta^{13}C$ alue. In 1981, however, vaseyana had the second ighest growth rate and isotopic value; yomingensis was lowest in both values. he rate of photosynthesis was highest in ccessions with high rates of growth, ranspiration, and $\delta^{13}C$ values. While hotosynthetic rates for all accessions followed transpiration rates, this correlation was not as strong as for $\delta^{13}C$ values and transpiration rates.

The average photosynthetic rate was higher in June than in August. Transpiration was also greater in June than in August. This trend in transpiration could be seen at the level of subspecies and accessions as well. As can be seen in figure 2, $\delta^{13}C$ values decreased from June to August.

Comparison of $\delta^{13}C$ values and transpiration rates among the subspecies showed a tendency for $\delta^{13}C$ values to become more negative as transpiration increased (fig. 2). The growth rate of each subspecies is given in figure 3; tridentata had the highest growth rate followed by wyomingensis and vaseyana.

Table 2.--Growth rates and $\delta^{13}C$ values for three subspecies of big sagebrush for 1981 and 1982. All values ± one standard deviation

	1981		1982	
Subspecies	$\delta^{13}C$ o/oo[1]	Growth rate[2] (cm/yr)	$\delta^{13}C$ o/oo[3]	Growth rate[4] (cm/yr)
tridentata	-27.6 ± 1.14	28.8 ± 8.70	-28.2 ± 1.08	32.7 ± 7.91
vaseyana	-28.0 ± 0.95	23.3 ± 6.14	-29.3 ± 0.78	21.6 ± 2.27
wyomingensis	-28.2 ± 0.87	20.1 ± 3.27	-28.7 ± 0.62	26.4 ± 6.23

[1] Means are significantly different at P <0.25.
[2] Means are significantly different at P <0.005.
[3] Means are significantly different at P <0.10.
[4] Means are significantly different at P <0.025.

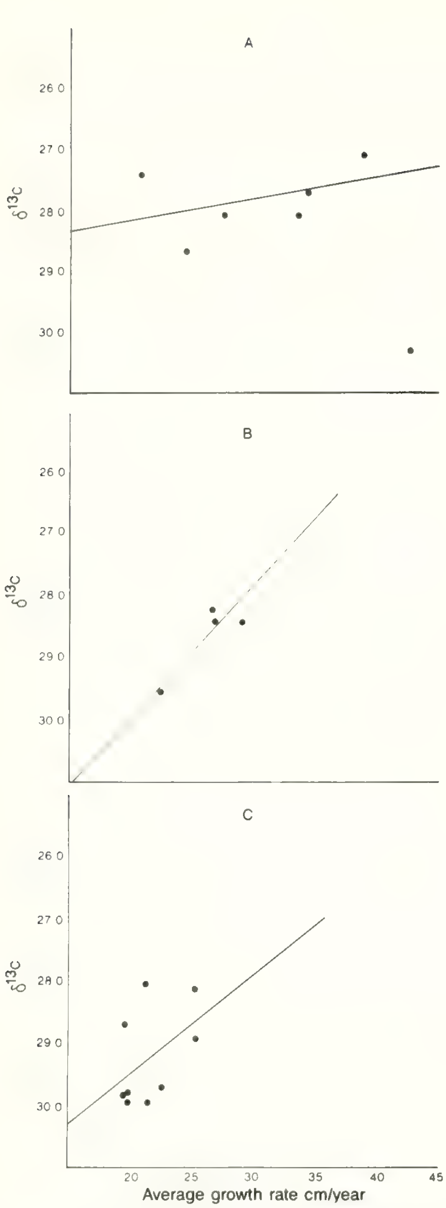

Figure 1.--Average growth rate (1982 vs. $\delta^{13}C$ in the three subspecies of Artemisia tridentata: (a) tridentata, (b) wyomingensis, (c) vaseyana. All three subspecies show a positive correlation: as $\delta^{13}C$ increases, growth rates also increase.

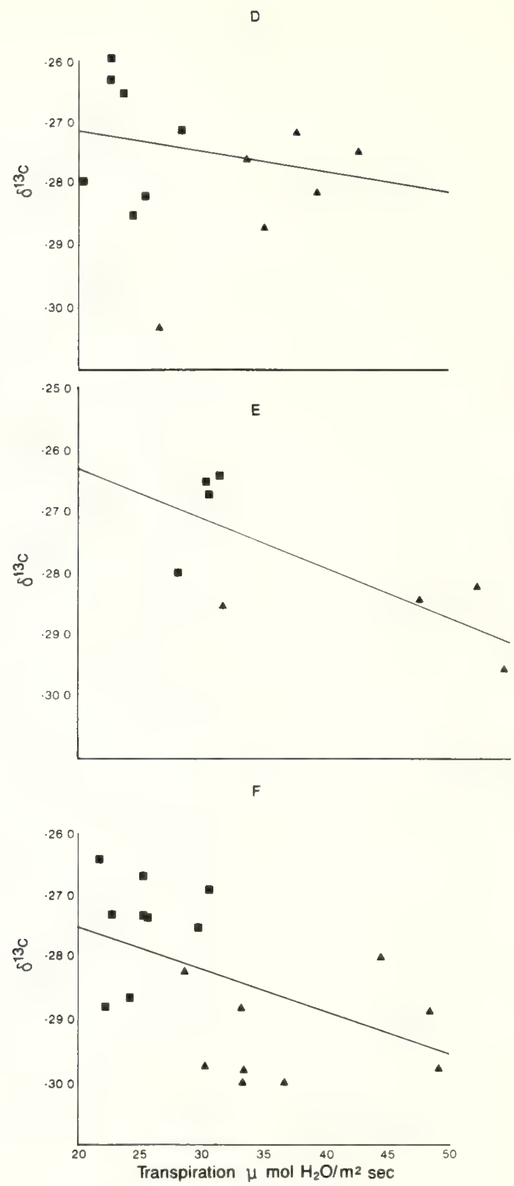

Figure 2.--Average $\delta^{13}C$ value vs. average transpiration rate in three subspecies of Artemisia tridentata: (d) tridentata, (e) wyomingensis, (f) vaseyana. All three subspecies show a negative correlation: as $\delta^{13}C$ increases transpiration decreases. Triangles represent June measurements and squares represent August measurements.

DISCUSSION

Theoretically there should be a close relationship between photosynthetic rate and dry matter production (Gaskel and Pearce 1981). Our results showed a direct relationship between growth rate and $\delta^{13}C$ values. As photosynthesis becomes more efficient, its $\delta^{13}C$ values became less negative.

Distribution of Artemisia tridentata subspecies occurs along a moisture gradient (McArthur 1983) (fig. 4). Presumably this distribution occurs because of genetic differences in environmental requirements since differences were maintained among subspecies when grown in a common garden (McArthur and Welch 1982). Genetic adaptation to different environments can be reflected in $\delta^{13}c$ values (Smith and others 1976). Vaseyana generally grows in cooler, more mesic sites than the other two subspecies. Its need to reduce water loss would, therefore, be less than that of wyomingensis which is adapted to harsh, dry soils, or tridentata which is found in the heat of the lower elevations (fig. 4). Vaseyana would not have to be as conservative with moisture. Tridentata, on the

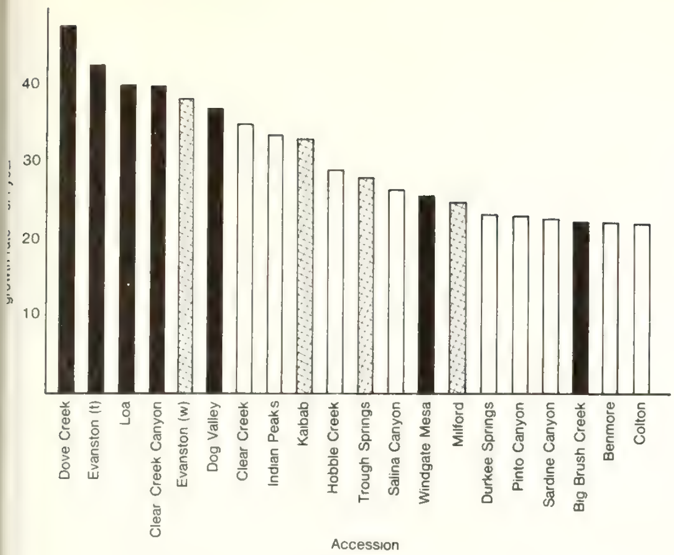

Figure 3.--Maximum growth rates attained by each accession. Solid bars, tridentata; hatched bars, wyomingensis; and open bars, vaseyana.

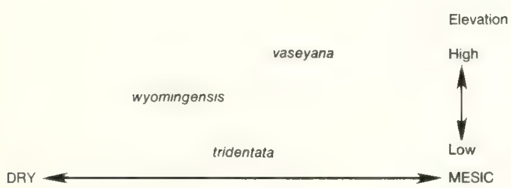

Figure 4.--Distribution of Artemisia tridentata subspecies along a moisture gradient in combination with elevation (McArthur 1983).

other hand, would require a greater water use efficiency. This, too, is reflected in higher $\delta^{13}C$ values and higher growth rates for tridentata. Wyomingensis generally grows on drier sites than tridentata, but at higher elevations with different precipitation patterns and soil conditions.

Subspecies of big sagebrush that exhibit rapid growth also show high rates of photosynthesis (reflected in less isotopic fractionation) and high rates of transpiration. Late summer rates of photosynthesis and transpiration were less than those measured in the spring perhaps due to decreased water availability. A general correlation was noted between photosynthesis, transpiration, and conditions at sites where the three subspecies naturally occur.

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COMPARISON OF PRODUCTION IN TWENTY-SEVEN

ACCESSIONS OF FOUR SAGEBRUSH TAXA

James N. Davis and Richard Stevens

ABSTRACT: Vegetative production was compared on an equal annual stem length basis for 27 accessions of four sagebrush taxa, black sagebrush (Artemisia nova), and three subspecies of big sagebrush (A. tridentata), grown in a common garden at Ephraim, UT. Production was a measure of oven dried weight, stem weight, and total weight (stem and leaf material together) per cm of annual leader growth. There were few singularly outstanding accessions evident but there were some consistent trends. A trend index value was used to help indicate each accession's overall level of performance. The amount of variation between species and among accessions of sagebrush on an equal length basis was significant. In general, when comparing the production of the four sagebrush taxa on the basis of equal annual leader lengths A. tridentata ssp. vaseyana > A. tridentata ssp. tridentata > A. tridentata ssp. wyomingensis > A. nova.

INTRODUCTION

Considerable effort has been put into sagebrush research. Early work emphasized sagebrush control to help improve livestock ranges. More recent research has recognized many positive values for planting sagebrush (McArthur and Plummer 1978). Sagebrush has been shown to be one of the most important browse plants for wintering mule deer in many Intermountain areas (Leach 1956; Plummer and others 1968; Robinette 1977; Tueller 1979). Sagebrush is highly variable in many morphological and physiological characteristics (McArthur and others 1979; Johnson 1983). For example, sagebrush has been shown to have considerable variation in digestibility (Welch and Pederson 1981), growth rate and size (McArthur and Welch 1982), crude protein (Welch and McArthur 1979), and preference (Welch and others 1983). Many improvements can be selected for through this high amount of variation that occurs within and between sagebrush taxa.

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Preference is an important characteristic to take into consideration when choosing species and/or accessions for seeding or outplanting, but the literature relating to preferential use is inconclusive with regard to the factors correlated to preferred use (Narjisse 1981; Radwan and Crouch 1978; Scholl and others 1977; White and others 1982). Preference has often been equated to the amount or percent use of the annual leader growth. These measurements have been used by researchers to make comparisons among taxa and accessions, and among years on critical wintering areas. These measurements have helped managers to set guidelines on how much use of the shrub annual leader growth can be consumed and still maintain plant vigor. But, percent use does not provide information on the amount of forage produced and consumed per plant. The problem of differing plant size is usually apparent and can be corrected for. Percent use when used for comparisons between different sagebrush accessions or taxa assumes that annual leader growth between and among taxa is the same, this could lead to some problems if not corrected for or recognized. Equal lengths of plant material have also been assumed equal in weight; they are not. Plant size differences have a strong genetic component and are important in annual forage production (McArthur and Welch 1982; Barker and others 1983). This could be an important concept to consider when choosing accessions for outplanting because forage production could be increased without increasing plant size or numbers. This study was designed to show if there are differences in production among or between sagebrush taxa when they are compared on the basis of adjusted equal annual leader lengths.

METHODS

Four taxa were chosen because of their natural abundance, use by wildlife, and availability within the same common garden at Ephraim, UT. They included: nine accessions of basin big sagebrush (Artemisia tridentata ssp. tridentata), four accessions of Wyoming big sagebrush (A. tridentata ssp. wyomingensis), seven accessions of mountain big sagebrush (A. tridentata ssp. vaseyana), and seven accessions of black sagebrush (A. nova) (table 1).

Five plants from each accession were randomly chosen from a common garden at Ephraim, UT, in late October of 1982. Four complete branches were randomly clipped off and separated into

Table 1.--Locations for sources of accessions of sagebrush taxa

Species	Subspecies	Accession	Location	County, State
tridentata	*tridentata*	U- 6	Snow Creek	Humbolt Co., NV
		U- 50	Fremont Road	Sevier Co., UT
		U- 55	Leonard Creek	Humbolt Co., NV
		U- 70	Moab	Grand Co., UT
		U- 74	Dove Creek	Dolores Co., CO
		U- 76	Clear Creek	Sevier Co., UT
		U- 79	Dog Valley	Juab Co., UT
		U- 82	Big Brush Creek	Uintah Co., UT
		U-107	Highway 28	Sweetwater Co., WY
tridentata	*wyomingensis*	U- 1	Trough Springs	Humbolt Co., NV
		U- 8	80/189 interchange	Uinta Co., WY
		U- 9	Milford	Beaver Co., UT
		U- 10	Decker Mine	Big Horn Co., MT
tridentata	*vaseyana*	U- 1	Hobble Creek	Utah Co., UT
		U- 9	Ephraim Canyon	Sanpete Co., UT
		U- 15	Sardine Canyon	Cache Co., UT
		U- 19	Salina Canyon	Sevier Co., UT
		U- 23	Pinto Canyon	Washington Co., UT
		U- 63	Carey	Blaine Co., ID
nova		U- 5	Manti	Sanpete Co., UT
		U- 7	Gunnison	Sanpete Co., UT
		U- 14	Alton (south)	Kane Co., UT
		U- 15	Alton (west)	Kane Co., UT
		U- 17	Desert Range	Millard Co., UT
		U- 18	Pine Valley	Millard Co., UT
		U- 22	Steinakers Res.	Uintah Co., UT

stems and leaves. Total stem length was measured to the nearest centimeter. The stems and leaves were oven dried and weighed separately. The data were summarized in tabular form in the following categories: weight of leaves per cm of stem, weight of stems per cm, total weight (stems and leaves) per cm of stem, and leaf weight as a percent of total weight. Categories for leaf weight, stem weight, and total weight will total correctly except for some small rounding errors. Percent leaf weight, however, sometimes will be slightly off the arithmetic totals from the table data because percent leaf weight was done on an equally weighted basis. All weights are in grams. A nested analysis of variance model was used (SAS User's Guide: Statistics 1982). A Newman-Kuel multiple means comparison test was used when there were significant differences among the means (Steel and Torrie 1960).

A trend index was used to better describe which accessions performed the best. This was done by giving each accession or species a score of 1 through n. The score received depended on its placement with regard to the others in the group, one point for first (the highest weight value), two points for second (the second highest weight value), etc. Each species' or accession's scores were summed for all categories. The species or accession with the smallest score was considered the best or most productive.

RESULTS

There were significant differences among the selected taxa of sagebrush (table 2). There was no one decidedly superior taxa in each category, but a definite trend was evident. Mountain big sagebrush was the most productive in all categories except for percent leaf weight. It had a trend index value of 5 out of a possible best score of 4 points. Mountain big sagebrush was 14 percent more productive than basin big sagebrush, 17 percent more productive than Wyoming big sagebrush, and 43 percent more productive than black sagebrush when compared on an equal length basis.

Basin Big Sagebrush

There were significant differences among accessions within the taxa. There was no decidedly superior basin big sagebrush (table 3), but for three of the four categories, the Clear Creek (U-76), Snow Creek (U-6), and Wyoming (U-107) accessions were consistently among the best. The one category in which two of these three accessions were not the best was weight of stems per cm. It is interesting to note that if you take the mean of the three best accessions, it was 21 percent more productive than the closest accession to it in total production and 37 percent more productive than the Fremont Road accession which is the lowest in total production. The trend index

Table 2.--Vegetative production (oven dry weights in grams) comparisons for equal stem lengths among four sagebrush taxa[1]

	ARTR^v	ARTR^t	ARTR^w	ARNO
Weight of leaves per cm	.193	.186	.147	.094
	ARTR^v	ARTR^w	ARTR^t	ARNO
Weight of stems per cm	.152	.145	.117	.106
	ARTR^v	ARTR^t	ARTR^w	ARNO
Total weight per cm	.346	.303	.293	.200
	ARTR^t	ARTR^v	ARTR^w	ARNO
Percent leaf weight	60.5	54.0	49.5	45.1
	ARTR^v	ARTR^t	ARTR^w	ARNO
Trend Index values[2]	5	8	11	16

[1]The means connected by a line are not significantly different at the .05 percent level. ARTR^t=basin big sagebrush, ARTR^w=Wyoming big sagebrush, ARTR^v=mountain big sagebrush, ARNO=black sagebrush

[2]Lower values indicate higher overall productivity (minimum value=4, maximum value=16).

scores ranged from 8 to 30. The three best accessions had trend index scores of 8 (Clear Creek), 11 (Snow Creek), and 12 (Wyoming).

Mountain Big Sagebrush

Low-elevation ecotypes of mountain big sagebrush have some of the best potential because of their apparent preferential use by wintering mule deer (Welch and others 1981). In general, either Pete Bishop (U-9) or Hobble Creek (U-1) were the best performing accessions of mountain big sagebrush (table 4). Accessions Pete Bishop (U-9) and Hobble Creek (U-1) had trend index values of 11 and 14, respectively, among values ranging from 1 to 30. To help illustrate the variability in total production between accessions, Pete Bishop (the most productive) was 42 percent more productive than Pinto Canyon (the least productive) when equal lengths were compared.

Wyoming Big Sagebrush

There was no decidedly superior Wyoming big sagebrush accession, but there was a noticeable trend. The Trough Springs (U-1) and Highway Interchange (U-8) accessions were the top two in three of the four categories with trend indexes of 6 and 9 respectively (table 5). Trend index values ranged from 6 to 15. With these two accessions producing a mean total weight of 0.362 grams per cm, they were 31 percent more productive than the Milford accession (U-9) and 48 percent more productive than the Decker Mine accession (U-10).

Table 3.--Vegetative production (oven dry weight in grams) comparisons of equal stem lengths for accessions of basin big sagebrush[1]

	ACCESSIONS								
	U-76	U107	U- 6	U-79	U-70	U-55	U-74	U-50	U-82
Weight of leaves per cm	.272	.261	.225	.173	.171	.168	.161	.127	.118
	U- 6	U-55	U-74	U-82	U-76	U107	U-79	U-50	U-70
Weight of stems per cm	.139	.130	.124	.118	.114	.112	.110	.108	.099
	U-76	U107	U- 6	U-55	U-74	U-79	U-70	U-82	U-50
Total weight per cm	.386	.374	.364	.298	.286	.283	.270	.236	.235
	U-76	U107	U-70	U- 6	U-70	U-74	U-55	U-50	U-82
Percent leaf weight	70.0	67.1	63.2	61.3	59.1	56.4	56.3	53.0	50.4
	U-76	U- 6	U107	U-55	U-74	U-79	U-70	U-82	U-50
Trend index values[2]	8	11	12	19	21	22	24	30	33

[1]The means connected by a line are not significantly different at the .05 percent level.
[2]Lower values indicate higher overall productivity (minimum value=4, maximum value=36).

able 4.--Vegetative production (oven dry weight in grams) comparisons for equal stem lengths among accessions of Mountain big sagebrush[1]

	ACCESSIONS						
	U- 9	U- 1	U-13	U-15	U-23	U-63	U-19
eight of leaves per cm	.324	.212	.180	.169	.161	.150	.148
	U-15	U- 1	U-19	U-63	U- 9	U-13	U-23
eight of stems per cm	.190	.170	.168	.155	.152	.130	.115
	U- 9	U- 1	U-15	U-19	U-13	U-63	U-23
otal weight per cm	.447	.382	.359	.316	.310	.306	.276
	U- 9	U-23	U-13	U- 1	U-63	U-15	U-19
ercent leaf weight	67.3	55.5	55.1	54.1	51.0	46.3	45.7
	U- 9	U- 1	U-15	U-13	U-63	U-19	U-23
rend index value[2]	11	14	18	23	24	28	29

The means connected by a line are not significantly different at the .05 percent level.
Lower values indicate higher overall productivity (minimum value=4, maximum value=28).

lack Sagebrush

o one accession of black sagebrush was ignificantly more productive, but the trend was or Walt James (U-17), West Alton (U-15), and teinakers Reservoir (U-22) to be the most roductive (table 6). They had trend index alues of 9, 10, and 12 respectively. Trend ndex values ranged from 9 to 24. The Walt ames (U-17) accession was 46 percent more roductive than the Manti accession (U-5), when hey were compared on an equal basis.

ISCUSSION

iterature on sagebrush has generally shown that here are usually clear choices as to which pecies or accession is the most preferred. owever, no one has been able to determine which omponents of sagebrush affect its preferential se by wildlife. Maybe these results can give ome explanation why this is so. When reference is determined by measuring percent emoval of the current year's growth and also by ssuming that equal stem lengths weigh the ame, these assumptions could confound the esults. For example, if two accessions (Pinto anyon and Ephraim Canyon) of the same taxon and bout the same size with average annual leader rowths of 9.3 and 8.2 cm respectively (McArthur nd Welch 1982) were both utilized at 5 cm, the phraim Canyon accession would have still rovided 42 percent more forage. A correction actor is necessary to take into account total se per plant. Such a factor could be etermined by sampling each accession or species nd obtaining a value for oven dried weight per nit of stem length. This could be used to etermine the differences in use (actual weight); the amount used could then be adjusted by this weight correction factor, allowing for a more accurate determination of how much of each species or accession has been consumed. This study showed that each accession and taxa does differ in productivity on a per unit length basis.

Table 5.--Vegetative production (oven dry weight in grams) comparisons for equal stem lengths among accessions of Wyoming big sagebrush[1]

	ACCESSIONS			
	U- 1	U- 8	U- 9	U-10
Weight of leaves per cm	.207	.145	.143	.093
	U- 8	U- 1	U- 9	U-10
Weight of stems per cm	.199	.172	.106	.105
	U- 1	U- 8	U- 9	U-10
Total weight per cm	.379	.344	.250	.198
	U- 9	U- 1	U-10	U- 8
Percent leaf weight	55.7	53.5	46.4	42.2
	U- 1	U- 8	U- 9	U-10
Trend index value[2]	6	9	10	15

[1]The means connected by a line are not significantly different at the .05 percent level.
[2]Lower values indicate higher overall productivity (minimum value=4, maximum value=16).

Table 6.--Vegetative production (oven dry wright in grams) comparisons for equal stem lengths among accessions of black sagebrush[1]

	ACCESSIONS						
	U-17	U-22	U-15	U-18	U- 7	U-14	U- 5
Weight of leaves per cm	.121	.115	.110	.101	.074	.070	.067
	U-15	U-22	U-17	U-14	U-18	U- 5	U- 7
Weight of stems per cm	.154	.129	.121	.111	.080	.076	.073
	U-15	U-22	U-17	U-18	U-14	U- 7	U- 5
Total weight per cm	.264	.244	.242	.181	.181	.147	.143
	U-18	U-17	U- 7	U- 5	U-15	U-22	U-14
Percent leaf weight	55.4	49.2	48.2	45.5	40.5	40.1	36.7
	U-17	U-15	U-22	U-18	U- 7	U-14	U- 5
Trend index value[2]	9	10	12	14	21	22	24

[1]The means connected by a line are not significantly different at the .05 percent level.
[2]Lower values indicate higher overall productivity (minimum value=4, maximum value=28).

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GROWTH RATE OF BIG SAGEBRUSH AS INFLUENCED BY ACCESSIONS, SITES, SUBSPECIES, AND YEARS

Bruce L. Welch and E. Durant McArthur

ABSTRACT: To aid in the development of improved cultivars of big sagebrush (Artemisia tridentata) for use on mule deer winter ranges, growth rate tests were conducted on accessions grown in a uniform garden. Genetically superior accessions were identified. To determine if genetic superiority is maintained in native stands, 21 accessions then were established on three different range sites. All three subspecies of A. tridentata were represented. Current-year leader growth was measured on each site for 5 years. Statistical tests detected significant ($P < 0.05$) effects due to accessions, sites, subspecies, and years. Genetic superiority, as determined under uniform garden conditions, was maintained across accessions, sites, subspecies, and years.

INTRODUCTION

Big sagebrush (Artemisia tridentata Nutt.) is the single most used winter mule deer (Odocoileus hemionus hemionus) forage in the Great Basin area of the Western United States (Leach 1956; Plummer and others 1973; Tueller 1978; Tisdale and Hironaka 1981; Blaisdell and others 1982). Because it is used so intensively, several characteristics of accessions of big sagebrush grown in uniform gardens are being studied by Forest Service and Utah Division of Wildlife Resources scientists (Welch and McArthur 1979; Welch and others 1981; McArthur and Welch 1982). The principal aim is to develop superior cultivars of big sagebrush for use on mule deer winter ranges. Characteristics being studied under winter conditions are: in vitro digestibility, crude protein content, monoterpenoid content, browsing preference, drought resistance, site adaptation, disease and insect resistance, seedling vigor, establishment methods, and annual growth rates or production. The last characteristic, growth rate, is the subject of this report.

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Other studies have demonstrated significant genetic growth rate differences among accessions and subspecies of big sagebrush growing in a uniform garden (Welch and McArthur 1979; McArthur and Welch 1982). The most productive accessions were of the subspecies tridentata (McArthur and Welch 1982). The apparent genetic growth rate superiority of the Dove Creek accessions (subspecies tridentata) was maintained on two other sites (McArthur and Welch 1982). Our purpose was to: (a) expand the knowledge base concerning the growth rates of 21 accessions of big sagebrush as influenced by site with age held constant, and (b) choose superior accessions for a breeding and selection program.

MATERIALS AND METHODS

Three outplanting sites were selected within the elevational range of most Utah mule deer winter ranges (1 370-2 140 m): near Springville, UT; 3 km east of Nephi, UT (Salt Creek Canyon); and 15 km west-southwest of Helper, UT (Gordon Creek Wildlife Management Area).

The Springville site at 1 402 m, is a basin big sagebrush habitat type. Soil is Pleasant Grove gravelly loam, 6 to 10 percent slope, with deep, well-drained, gravelly or cobbly soils on alluvial fans. Weathered limestone is the parent material. Soil permeability is moderately rapid. Roots can penetrate to a depth of 1.5 m or more. About 9 cm of available water is held by this soil to a depth of 1.5 cm. Soil pH ranges from 7.4 to 7.9. Average annual precipitation is 35 to 45 cm. The mean annual temperature is 8.9 to 11.1°C, and the frost-free period is 150 to 170 days (Swenson and others 1972).

The Salt Creek Canyon site (1 676 m) is a basin big sagebrush habitat type. Soil is a Rofiss gravelly clay loam, 4 to 15 percent slope. It is a deep, well-drained alluvial soil. Parent material is Arpien shale. Soil permeability is moderately slow. Effective rooting depth is 1.5 m or more. Soil pH ranges from 8.2 to 8.6. Average annual precipitation is 30 to 35 cm. The mean annual temperature is 7.2 to 8.3°C, and the frost-free period is 100 to 120 days (Soil Conservation Service 1981).

The Gordon Creek Wildlife Management Area, at 2 130 m, is a Wyoming big sagebrush habitat type. Soil is of the Atrac series (Atrac very fine sandy loam, 1 to 6 percent slopes). This series consists of deep, well-drained soils. Parent material is sandstone. Effective rooting depth is 1.5 m or

more. Soil pH ranges from 6.6 to 8.0. Average annual precipitation is 30.5 to 35.6 cm. The mean annual temperature is 7.2 to 8.3°C, and the frost-free period is 100 to 120 days (Soil Conservation Service 1981).

At each site, the vegetation was killed by disking. Subsequent weeds were removed by hand and mechanical means. Deer-proof fences were built around each site. Each site was planted (spring 1978) with containerized stock of 21 accessions of big sagebrush. Table 1 lists the accession collection sites. Each accession was represented by 10 plants and each plant was an experimental unit within the accession. The resulting 210 plants were placed at random on a 3- by 3-m grid for each site.

Two three-way analyses of variance ($P < 0.05$) were performed on the data collected. Main effects for the first were sites, year, and accessions. For the second, the main effects were sites, year, and subspecies. Newman-Keuls multiple range test ($P < 0.05$) was used to compare treatment means.

RESULTS AND DISCUSSION

The overall mean big sagebrush annual leader length for all years, sites, and accessions was 22.9 cm. The two three-way analyses of variance detected

Table 1.--Collection sites for 21 accessions of big sagebrush used to determine the influence of site on growth rates

Subspecies	Accessions	County and State	Elevation
			(m)
vaseyana	Colton	Utah, UT	2260
	Sardine Canyon	Cache, UT	1800
	Benmore	Tooele, UT	1900
	Petty Bishop's Log	Sanpete, UT	2380
	Durkee Springs	Sevier, UT	2270
	Salina Canyon	Sevier, UT	2130
	Clear Creek Canyon	Sevier, UT	2130
	Pinto Canyon	Washington, UT	1850
	Indian Peaks	Beaver, UT	2140
	Hobble Creek	Utah, UT	1500
tridentata	Clear Creek Canyon	Sevier, UT	1720
	Big Brush Creek	Uintah, UT	1830
	Loa	Wayne, UT	2140
	Evanston	Uinta, WY	2020
	Wingate Mesa	San Juan, UT	2060
	Dog Valley	Juab, UT	1700
wyomingensis	Evanston	Uinta, WY	2130
	Kaibab	Coconino, AZ	2340
	Trough Springs	Humboldt, NV	1400
	Milford	Beaver, UT	1540

Growth rates were determined by measuring the annual length of 15 leaders per plant. Leader lengths were measured from the terminal leaf bud scars to the tip of the current terminal leaves. Leaders were selected at random over the entire crown of the plant. The 15 measurements were pooled together to calculate a plant mean. Measurements were taken during mid-November in 1979, 1980, 1981, and 1982. For the first year (1978) plant height was considered to be the height of the transplanted seedling.

The three subspecies of big sagebrush, *Artemisia tridentata* ssp. *tridentata*, ssp. *vaseyana*, and ssp. *wyomingensis*, were represented in this study. Of the 21 accessions, 10 were *vaseyana*, seven were *tridentata*, and four were *wyomingensis*. This gave the capability of testing for subspecies effects on growth rates.

effects due to all variables--year, site, subspecies, and accession.

The mean annual leader length for 1978 (24.1 cm) was significantly greater than for 1980 and 1981 (table 2). Annual leader lengths for 1979 and 1982 were not significantly less than 1978.

The Gordon Creek site produced smaller annual leader length (22.0 cm) than the Springville and Salt Creek sites (table 3).

Subspecies *wyomingensis* (17.3 cm) produced less leader length than subspecies *vaseyana* and *tridentata* (table 4). Subspecies *vaseyana* (20.4 cm) produced less leader length than subspecies *tridentata*.

Table 2.--Mean annual leader length of 210 big sagebrush plants grown for 5 years at three sites. Data are expressed as centimeters of current year's growth

	Years				
	1978	1979	1980	1981	1982
Length (cm)	24.1^{c*}	22.9^{abc}	21.5^{a}	22.5^{ab}	23.7^{bc}

*Means sharing the same superscript are not significantly different ($P < 0.05$).

Table 3.--Mean annual leader lengths of 210 big sagebrush plants grown for 5 years at three sites. Data are expressed as centimeters of current year's growth

	Site		
	Gordon Creek	Springville	Salt Creek
Length (cm)	22.0^{a*}	23.0^{b}	23.8^{b}

*Means sharing the same superscript are not significantly different ($P < 0.05$).

Table 4.--Subspecies mean annual leader lengths of big sagebrush plants grown for 5 years at three sites. Data are expressed as centimeters of current year's growth

	Subspecies		
	wyomingensis	vaseyana	tridentata
Length (cm)	17.3^{a*}	20.4^{b}	29.6^{c}
Number of plants per subspecies	120	300	210

*Means sharing the same superscript are not significantly different ($P < 0.05$).

The Dove Creek accession (41.4 cm) produced more annual leader length than the other accessions. Dove Creek represents subspecies tridentata (table 5). Other subspecies tridentata accessions with significantly longer leader lengths than vaseyana and wyomingensis accessions were Loa, Dog Valley, Evanston, and Clear Creek Canyon. Pinto Canyon (23.2 cm), Hobble Creek (23.1 cm), Salina Canyon (23.0 cm), and Indian Peaks (22.4 cm) were the fastest growing accessions of subspecies vaseyana.

Also, the three-way analyses of variance detected significant two-way interactions between site:accession and year:accession. Data shown in tables 6 and 7 explain the reason for the interactions. Across sites (table 6), some shifting in the ranking of accessions occurred.

Table 5.--Mean leader lengths of 21 accessions of big sagebrush grown on three sites for 5 years (10 plants per accession per site). Data are expressed as centimeters of current year's growth

Accession	Length (cm)
Petty Bishop's Log (v)*	15.3^{a**}
Trough Creek (w)	15.5^{a}
Evanston (w)	15.8^{a}
Big Brush Spring (t)	16.7^{ab}
Colton (v)	17.2^{ab}
Milford (w)	17.2^{ab}
Benmore (v)	18.8^{bc}
Clear Creek Canyon (v)	20.1^{cd}
Sardine Canyon (v)	20.2^{cd}
Durkee Springs (v)	20.6^{cde}
Kaibab (w)	20.7^{cde}
Wingate Mesa (t)	20.9^{cde}
Indian Peaks (v)	22.4^{def}
Salina Canyon (v)	23.0^{ef}
Hobble Creek (v)	23.1^{ef}
Pinto Canyon (v)	23.2^{f}
Clear Creek Canyon (t)	30.8^{g}
Evanston (t)	30.9^{g}
Dog Valley (t)	33.0^{h}
Loa (t)	33.1^{h}
Dove Creek (t)	41.4^{i}

* v = Artemisia tridentata ssp. vaseyana, w = ssp. wyomingensis, t = ssp. tridentata.

** Means sharing the same superscript are not significantly different ($P < 0.05$).

This shifting also occurred across years (table 7). The shifting caused the interactions to be statistically significant. However, the Dove Creek accession maintained its genetically superior growth rate on all three sites and across all 5 years (tables 6 and 7). This strengthens our justification for including the Dove Creek accession in our selection and breeding program (Welch and McArthur 1979; McArthur and Welch 1983).

The Hobble Creek accession maintained its ranking among the fastest growing vaseyana on all sites and for the first 3 years (tables 6 and 7. Our interest in the Hobble Creek accession stems from its high browse preference ranking (Welch and others 1981).

This study, along with others demonstrates that growth rate differences among subspecies and accessions of big sagebrush reflect genetic influences (Welch and McArthur 1979; Barker 1981; McArthur and Welch 1982). The plants maintain growth pattern differences in native stands as well as in uniform gardens.

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Table 6.--Ranking (out of 21) and mean annual leader growth of six accessions of big sagebrush grown on three sites. Data represent a 5-year average. Data are expressed as centimeters of current year's growth

Site	Accessions											
	Dove Creek		Hobble Creek		Pinto Canyon		Salina Canyon		Petty Bishop's Log		Trough Creek	
	R*	L**	R	L	R	L	R	L	R	L	R	L
Gordon Creek	1	40.4	6	23.0	7	22.8	9	20.4	16	16.4	21	14.5
Springville	1	44.6	7	23.6	8	22.9	6	24.9	21	13.0	18	16.5
Salt Creek	1	39.3	9	22.6	6	23.9	7	23.9	20	16.3	21	15.3

*Ranking of 21 accessions.
**Mean accessional annual leader length for 5 years.

Table 7.--Ranking and mean annual leader growth of six accessions of big sagebrush grown on three sites. Data represent a three-site average. Data are expressed as centimeters of current year's growth

Year	Accessions											
	Dove Creek		Hobble Creek		Pinto Canyon		Salina Canyon		Petty Bishop's Log		Trough Creek	
	R*	L**	R	L	R	L	R	L	R	L	R	L
1978	1	41.3	7	27.5	8	25.8	6	27.6	15	19.7	19	14.1
1979	1	43.7	6	24.3	7	23.3	8	23.2	19	15.2	20	14.0
1980	1	40.2	6	22.2	8	20.7	9	20.4	21	14.1	20	14.6
1981	1	38.4	10	21.5	6	22.1	8	22.0	21	14.2	20	16.9
1982	1	43.7	12	19.6	6	24.3	9	21.8	21	12.9	17	18.2

*Ranking out of 21 accessions.
**Mean accessional annual leader length for three sites.

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GROWTH AND INTERNAL WATER STATUS OF THREE SUBSPECIES

OF ARTEMISIA TRIDENTATA

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BSTRACT: Plant growth, leaf senescence, plant ater potential, and soil water were measured or three subspecies of Artemisia tridentata. lant water potentials for the two subspecies rowing on the more mesic sites proved to be ore responsive to changes in climate. Persistent eaves remained on the plants for one winter nd two growing seasons.

NTRODUCTION

rtemisia tridentata dominates 90 million acres 36.5 million ha) in the Western United States, contituting the most abundant and widespread of he woody species characteristic of the extensive agebrush/grass region. Three taxa of A. tridentata ave been reported by Beetle (1960), Beetle nd Young (1965), Winward (1970), and Winward nd Tisdale (1977). They vary morphologically nd phenologically, and have distinct ecologic nd hydrologic requirements.

'axa studied were Artemisia tridentata subspecies ridentata (ARTRT), wyomingensis (ARTRW) and aseyana (ARTRV). A fourth subspecies spiciformis s described in this proceedings (see McArthur nd Goodrich) but was not a part of our study. 'he objectives of this study were to record lant growth, leaf abscission, and seasonal nd diurnal fluctuations in water potential f these subspecies and to relate these factors o air temperature and soil water.

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STUDY AREA

Work was conducted on the Squaw Butte Experimental Range, situated in southeastern Oregon on the northern fringe of the Great Basin. The study was conducted from mid-May 1981 through November 1982.

The 40-year mean precipitation on the area is 11.8 inches (30 cm). The 1980-81 and 1981-82 crop year (September 1-August 30) precipitation levels were 83 and 117 percent of the mean, respectively.

The three sites selected for study were representative of the following three habitat types (Doescher 1983): Artemisia tridentata ssp. wyomingensis-Stipa thurberiana, A. tridentata ssp. tridentata/Elymus cinereus, and A. tridentata ssp. vaseyana/Festuca idahoensis. Sites were all within 2 miles (3.2 km) of each other (table 1). Macroclimate and soils, except for soil depth and rock content, were similar among all three sites.

METHODS

Phenology for each subspecies was recorded once every 2 weeks from mid-May through November 1981 and March through November 1982. In 1982, stem elongation and leaf fall were also measured. Twenty stems were permanently marked on each site prior to plant growth, and length was measured weekly from March through November. To measure persistence and timing of winter-persistent leaf fall, approximately 300 overwintering leaves on each site were marked with ink in March 1982 prior to new leaf development. To evaluate the proportion of leaf biomass abscissing in August, cheesecloth leaf traps were placed over 10 individual branches just prior to initial leaf fall (August 1) on each site. Leaves collected in the traps were removed on August 16, dried for 48 hours at 140 °F (60 °C) and weighed. Leaves remaining on the stem were also removed at this time, dried, and weighed.

Table 1.--Vegetation and soil characteristics of the study area

Plant communities	Elevation	Shrub cover	Herbaceous biomass	Soil classification	Soil texture of surface horizon	Soil depth
	Feet	Percent	Lbs/acre			Inches
ARTRV/FEID	5,082	15	613	Typic Haploxeroll	Loam	60
ARTRT/ELCI	4,498	20	555	Xerollic Durorthid	Sandy Loam	47
ARTRW/STTH	4,498	15	545	Xerollic Durorthid	Sandy Loam	18.5

Internal stem xylem water potential (ψw) of the three subspecies was measured during the 1981 and 1982 growing seasons by means of a pressure bomb (Scholander and others 1965; Waring and Clary 1967). Units for ψw are expressed in Megapascals (MPa). Diurnal measurements were taken at 5 a.m., 8 a.m., 11 a.m., 2 p.m., and 5 p.m. at 2-week intervals from June through July and monthly from August through October in 1981. In 1982, measurements were taken at 2-week intervals from May through July and then monthly to November. Diurnal patterns reported in the text were selected to characterize different temperature and soil water conditions. All other diurnals recorded followed a similar pattern to those selected. Seasonal ψw measurements, expressed over time are for both predawn (5:00 a.m.) and midday (2:00 p.m.) measurements. Plant water potentials are generally highest (plant least stressed) during the predawn hours and lowest during midday when evaporative potentials are generally the highest. Foliar samples for ψw readings were enclosed in a moist plastic bag, placed on ice for all three sites and then measured in a pressure bomb within 0.5 hour of collection. Two readings on three shrubs for each subspecies were recorded for each determination. Each pair of readings was treated as a subsample in the analysis of variance. Mean squares for subsamples and sample units (shrubs) were pooled so sample size for ψw measurements was 6 rather than 3 for each subspecies (Steel and Torrie 1960). Mean ψw for similar dates between years, and predawn and midday ψw were compared with the Student t test ($P<0.05$)

Soil moisture was measured gravimetrically at two depths (1-12 inches [2.5-30 cm] and 12-18.5 inches [30-47 cm]) in the ARTRW habitat type, and three depths (1-12 inches [2.5-30 cm], 12-24 inches [30-60 cm], and 24-48+ inches [60-120+ cm]) in the ARTRT and ARTRV habitat types. Soil moisture was sampled in conjunction with ψw measurements. Soil moisture release curves were used to convert percent soil moisture to soil water potential for each site.

Temperature and precipitation data were collected by means of standard Weather Bureau instruments located within 2 miles (3.2 km) of all three study sites. Air temperatures were recorded on the individual sites, but did not vary more than 3.6 °F (2 °C) from the Squaw Butte weather station, or site to site.

RESULTS

Climate 1981 and 1982

The 1981 growing season was drier and warmer than the 1982 growing season (fig. 1). During the 1982 crop year, 4 inches (10.2 cm) more precipitation was received than in 1981, allowing greater recharge of soil water at the lower depths. Although June and July temperatures were similar in both years, August and September temperatures in 1981 were warmer. In 1981 and 1982, respectively, degree days (based on 65 °F [18.3 °C]) totaled 190 and 117 in August and 68 and 27 in September (National Oceanic and Atmospheric Administration 1981, 1982).

The relatively high soil moisture during early June 1981 (fig. 2 a, b, and c) can be accounted for by above-normal spring precipitation which resulted in a moist upper 12 inches (30 cm) of soil. However, the persistence of relatively high soil water later in the 1982 growing season, also shown in the figures, was due to more soil water being available at depths below 12 inches (30 cm) than in 1981.

Phenology and Growth

Sequence of phenological development was similar for all three subspecies (fig. 2). Timing of leaf and stem development was similar for ARTRW and ARTRT, while ARTRV lagged behind by 2 weeks. ARTRV caught up with the other two subspecies by late June. ARTRW slowed stem elongation earlier than the other two subspecies (fig. 3). The most rapid rate of vegetative stem elongation measured was 0.04 inches/day (1.0 mm) for both ARTRW and ARTRT, and 0.07 inches/day (1.8 mm) for ARTRV. Reproductive stems were differentiated by mid-June for all

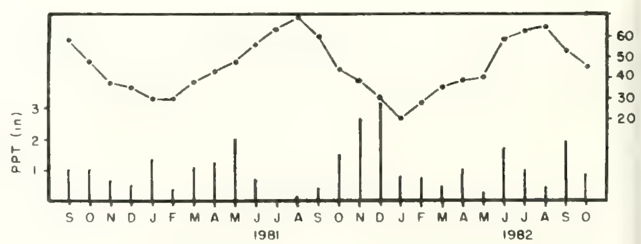

Figure 1.--Seasonal precipitation and maximum and minimum air temperatures for the Squaw Butte Experimental Range in 1981 and 1982.

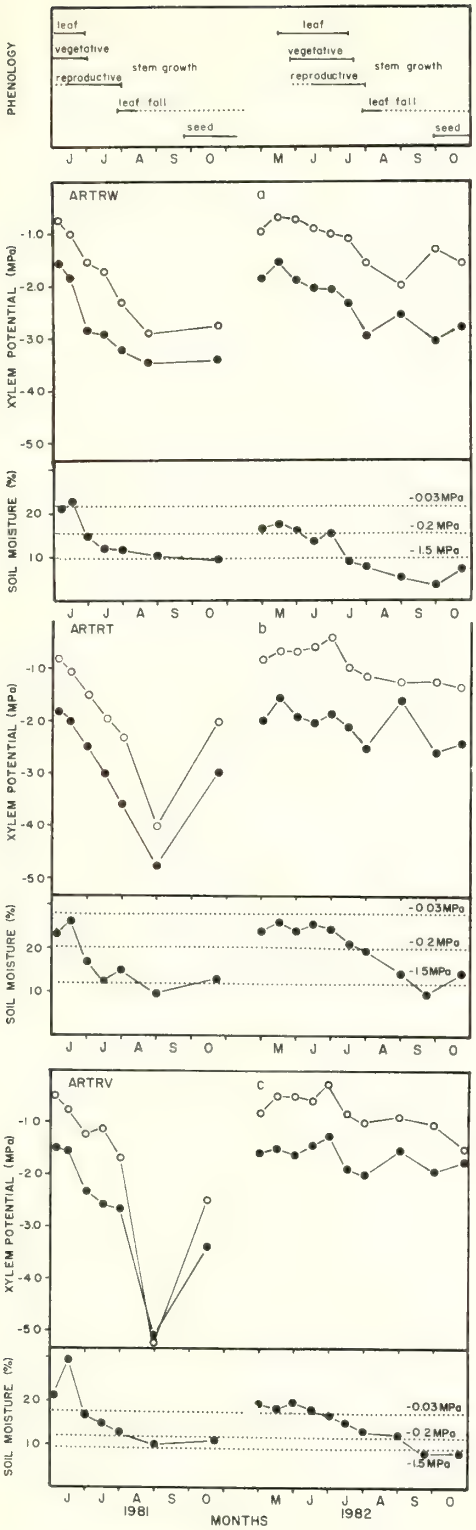

Figure 2.--Phenology and stem xylem water potential (MPa) and soil moisture in the wettest horizon on the site for two growing seasons for a) Wyoming big sagebrush (ARTRW), b) basin big sagebrush (ARTRT) and c) mountain big sagebrush (ARTRV). Plant phenology (----) for reproductive stems during the period they could not be separated from vegetative stems and leaf fall was minimal, restricted to ephemeral leaves.

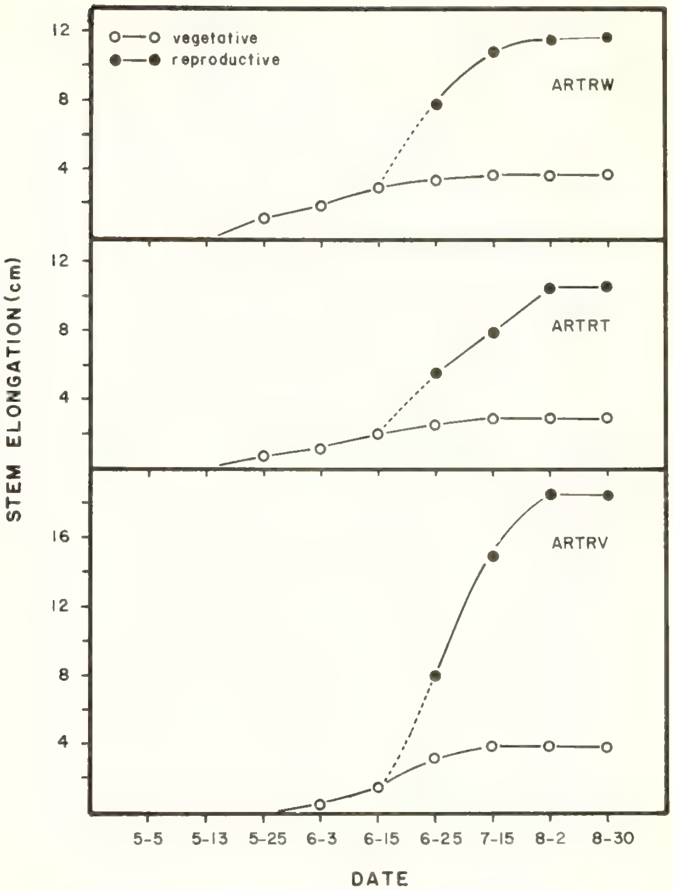

Figure 3.--Reproductive and vegetative stem elongation for the three subspecies during 1982.

three subspecies. At this time, vegetative stem elongation slowed down and terminated while reproductive stems rapidly grew for approximately 4 more weeks at maximum rates of 0.17, 0.15, and 0.25 inches/day (4.3, 3.8, and 6.4 mm) for ARTRW, ARTRT, and ARTRV, respectively. Although ARTRW reproductive stems grew at a faster rate than ARTRT, duration of rapid elongation was shorter. Termination of vegetative stem and leaf growth coincided with soil moisture tensions below -0.20 MPa.

Less than 2 percent of the marked winter persistent leaves fell from the plants between March and July on all three subspecies. During August, hot temperatures, low soil water, and low internal plant water potentials resulted in loss of 53 percent of the total leaf biomass on all three subspecies. Leaf senescence began in late July for ARTRW and ARTRT, with leaf abscission beginning by the first of August. The pattern was similar for ARTRV, however, the events occurred 10 days later. The entire crop of 1981-82 winter-persistent leaves fell in August 1982. The majority of ephemeral leaves also fell during this time. Ephemeral leaves continued to fall until early November, but at a slower rate. By late October, reproductive stems were leafless and drying on ARTRW and ARTRT, and seeds were in the hard dough stage. In contrast leaves on ARTRV reproductive stalks were falling, and seeds were in the dough stage.

Seasonal Water Potential

Predawn ψw during the two growing seasons ranged from -0.70 to -2.80, -0.45 to -3.90, and -0.34 to -5.80 MPa for ARTRW, ARTRT, and ARTRV, respectively (fig. 2a, b, and c). Midday ψw ranged from -1.45 to -3.44, -1.59 to -4.74, and -1.33 to -5.55 MPa for ARTRW, ARTRT, and ARTRV, respectively. Sharp declines in ψw occurred in both years for all three subspecies when soil water dropped below -0.20 MPa. Predawn ψw from July through October for ARTRW and mid-June through October for ARTRT and ARTRV were significantly less negative ($P<0.05$) in 1982 than 1981. The largest differences (significant at $P<0.05$) in ψw between years existed in ARTRT and ARTRV during late August and early September.

Diurnal Water Potential

Diurnal ψw patterns for the three subspecies of ARTR are represented in figures 4 and 5. The greatest differences (significant at $P<0.05$) between predawn and midday ψw occurred when soil moisture was readily available and midday temperatures were warm. When soil water was limited, as on August 31, 1981, little diurnal change occurred in ψw. The relationship of ψw between subspecies in late August was reversed between years. In 1981, ARTRW ψw were higher (least stressed) than ARTRT and ARTRV growing on the more mesic sites. In 1982, these results were reversed with ARTRV having the highest ψw in August. The data are interpreted to show: (1) a subspecies growing on a more mesic site may or may not have a lower water stress value, based on ψw, than subspecies growing on drier sites, and (2) the relative difference in ψw between subspecies can greatly change from year to year.

DISCUSSION

Phenology

The entire leaf crop which persisted through the winter was shed in late July and early August. Although leaves were not marked in 1983 and 1984, biweekly observations throughout the spring and summer, and monthly throughout the fall and winter on the Squaw Butte Experimental Range showed this pattern to be consistent. Spot checks throughout eastern Oregon also showed the leaf fall pattern to be similar. These data are interpreted to show winter-persistent leaves remain on the plant for two growing seasons and one winter. Abscission of winter-persistent leaves did not occur during the rapid growth phase of the plant. When soil water levels dropped below -0.20 MPa in the wettest horizon, vegetative stem elongation and leaf development terminated, and winter-persistent leaves began to senesce. These results are in contrast to Diettert (1938) and Branson and others (1976) who report that leaves persisting through the winter were shed in the spring as new leaves developed. Differences in leaf fall among these studies may be due to differences in location of plants studied. In eastern Oregon, springs

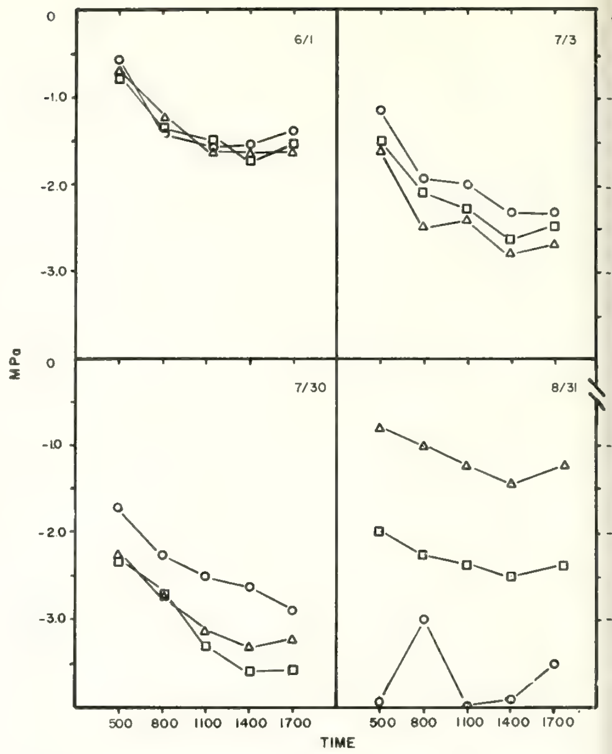

Figure 4.--Diurnal cycles of stem xylem water potentials in 1981 for Artemisia tridentata ssp. wyomingensis (△——△), tridentata (□——□) and vaseyana (○——○). Each point is a mean of six observations per time period.

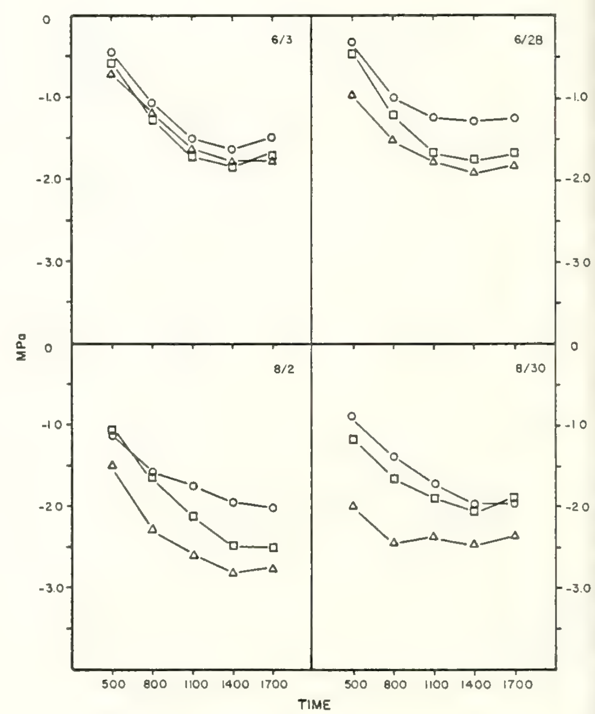

Figure 5.--Diurnal cycles of stem xylem water potentials in 1982 for Artemisia tridentata ssp. wyomingensis (△——△), tridentata (□——□), and vaseyana (○——○). Each point is a mean of six observations per time period.

a typically wet and summers dry. In Colorado w re the other two studies were conducted, s ings are relatively drier than summers. I addition we found 53 percent of the leaf b mass falling in early August (last year's p ennials plus current year's ephemerals) from t plant, whereas Branson and others (1976) e imated leaf fall as 85 percent of the total n ber of marked leaves. Because ephemeral l ves are initiated earlier than perennial l ves, and if the previous year's winter-persistent l ves are still present, the period when leaf m king is done will influence the proportion o leaf types in the sample. The number of p vious and current year's perennial leaves a the ephemeral leaves marked will determine t percent of marked leaves remaining on the p nt.

P nt Water Potentials

M imum and minimum ψw were consistent with o er work on A. tridentata (Barker and McKell 1 83; Branson and Shown 1975; Campbell and Harris 1 77; DePuit and Caldwell 1973; Dina and others 1 73; Everett and others 1977). DePuit and C ldwell (1973) suggested differences between m nimum ψw (-2.1 MPa) in their study and Dina's (70) results (-6.4 MPa) may have been due to c imatic conditions and location. In our study, s milar differences occurred between ARTRT and A TRV in 1981 and 1982, but on plants at the s me location. Minimum predawn ψw occurring i 1981 was -3.8 MPa for ARTRT and -5.8 MPa f r ARTRV. In contrast, -1.3 MPa for ARTRT a d -1.6 MPa for ARTRV occurred in 1982. Differ- e ces in minimum ψw between years in this study m y be attributed to more precipitation in 1982, c using greater soil moisture recharge at the d eper depths, and cooler temperatures in August a d September for 1982. This study would support t e hypothesis that climatic conditions have a m jor influence on minimum ψw occurring during t e growing season.

A though ARTRT is thought to exist on a more m sic site than ARTRW, ψw in 1981 did not reflect t is. In June, July, and August, ARTRT ψw were e ther similar or more negative than ARTRW values. T is may have been caused by the existence of a larger plant evaporative surface in the ARTRT c mmunity, which contained a taller canopy and g eater shrub canopy cover than ARTRW. In a y ar of poor soil water recharge at deeper soil d pths and high evaporative demands (1981), A TRT was more water stressed based on the than ARTRW. When adequate water was available 982), then ARTRT was the least water stressed the two. Although ARTRV ψw, in comparison the other two subspecies, was consistent th growing on a more mesic site early in the owing season, it had the lowest ψw in late gust 1981. Again, this may be attributed lack of soil water and a high plant evaporative rface (due to higher herbaceous productivity asured by Doescher, 1983) as compared to ARTRW. ller and Poole (1979) found a similar pattern the more mesic communities in southern California rublands, where both leaf area and internal ant water stress were greater than on the ier sites.

Differences in ψw for ARTRW were not nearly as great between years as they were for ARTRT and ARTRV (fig. 2 a, b, and c). ARTRW ψw did not seem to be as responsive to differences in climate between years as ψw of the other two subspecies. This may be due to several reasons:

1. Sites with shallower soils have more limited storage for above-average precipitation, as compared to sites with deeper soils.
2. More xeric communities have less evaporative surface (lower leaf area) and/or
3. subspecies may differ morphologically and/or physiologically.

CONCLUSIONS

Although big sagebrush is well adapted to arid environments, active vegetative growth occurred only at soil water tensions at or above -0.2 MPa. Soil water tensions between -0.03 and -0.2 MPa represent approximately 30 percent of the total water found in the soil profile. Once soil water decreased below -0.2 MPa, plant water potentials sharply decreased, active vegetative growth was terminated, and leaf abscission initiated. In August, plants reduced leaf biomass by over 1/2. Caldwell (1979), in a review of sagebrush physiology, reported photosynthesis is inhibited by moderate plant water stress. He speculated that success of the plant must depend on the display of numerous leaves during the cool season of the year when moisture stress had not yet developed. This would point out the importance of maintaining winter-persistent leaves throughout the spring.

Just because plants grow on a relatively more mesic site does not mean soil moisture will be higher or internal plant water stress less. These communities have developed strategies to exploit the larger available water resource by developing more extensive root systems and larger evaporative surfaces than more xeric communities. In years when precipitation doesn't fully recharge the soil, the more mesic communities may be subject to greater plant water stress.

Timing of abcission of the perennial leaves needs to be more thoroughly studied throughout the range of A. tridentata. In eastern Oregon, persistent leaves overwintered and fell from plants during the midsummer drought period of the following growing season.

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SEED PAPPUS AND PLACEMENT INFLUENCES ON WHITE RUBBER RABBITBRUSH ESTABLISHMENT

R. Stevens, K. R. Jorgensen, J. N. Davis, and S. B. Monsen

BSTRACT: Using present seed cleaning and eeding techniques, seedling establishment of hite rubber rabbitbrush from direct seeding as generally been poor. To facilitate andling and seeding, seed pappus is removed. eeds are generally broadcast seeded and eposited in or on the soil in no particular osition. Results indicate removal of seed appus reduces seedling establishment. reatest number of seedlings established when eeds were placed upright in the soil. Seeding echniques and equipment need to be developed hat will assure proper seed placement and aximum seedling establishment.

NTRODUCTION

hite rubber rabbitbrush (Chrysothamnus auseosus (Pallas) Britt. ssp. albicaulis Nutt.] Rydb.) is looked upon as a useful range hrub for livestock and wildlife (Hanks and thers 1975; McArthur and others 1978, 1979; asser 1982) and a useful species for tabilization (USDA 1974; McArthur and others 974, 1978; Thornburg 1982).

hite rubber rabbitbrush normally produces seed nnually. Seedlings naturally establish on angelands and reclamation sites, especially isturbed areas where competition is lacking or s slight (McArthur and others 1979). housands of seedlings can be found in bare and isturbed soils, under and next to mature lants. Most do not, however, develop beyond he seedling stage. Seedlings are not very ompetitive and may be suppressed by herbaceous pecies. In some cases, grass production can e enhanced in the presence of this overstory hrub (Plummer 1959; Frischknecht 1963; Plummer nd others 1968).

ith present seed cleaning and seeding echniques, establishment from direct seeding as been variable, but generally very poor.

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For example, Van Epps and Stevens (1984) planted 400,000 (estimated, number of seeds per gram) cleaned white rabbitbrush seeds (83 percent germination), each in three seeding treatments: (1) on top of undisturbed soil, (2) on top of undisturbed soil followed by disturbance, and (3) on top of disturbed soil followed by disturbance. Of the approximately 1.2 million seeds planted, less than 0.1 percent produced seedlings. Generally, with rabbitbrush, there is a great difference between the seedling potential and the actual number of seedlings established. King (1966) reported similar results with Taraxacum. Only 50-125 seedlings established for 10,000-20,000 seeds planted.

The fruit of rabbitbrush is technically a spindle-shaped achene (USDA 1974). For the purpose of discussion, we will consider an achene a seed. The terminal, or crown end of each seed bears a ring or crown of hairs, known as the pappus. The basal end includes the basal attachment scar.

Seed is generally hand-collected. To reduce volume and to facilitate handling and seeding, seed is run through a hammermill or debearder and screened and fanned to remove the pappus (USDA 1974; Plummer and Jorgensen 1978). Seed cleaned in this manner is 15 to 20 percent pure. With additional cleaning, seed can be cleaned up to 95 percent pure. Seed with less than 70 percent purity can only be seeded aerially, by hand, or through a thimble seeder. Seed over 70 percent pure can be drilled.

Two major differences between naturally seeded and artificially planted seed are the absence or presence of the seed pappus and subsequent placement of the seed in the soil. The pappus aids in wind dispersal of the seed (McArthur and others 1979). The presence of the pappus also aids in positioning a seed with the basal end down in contact with the soil. Seed can be deposited in soil cracks, cavities, or left lying on top of the soil. To maximize germination, the area of the seed that is the most efficient in absorbing water should be in contact with the growth medium. Sheldon (1977) reported that Taraxacum officinale is very sensitive to seed position. The highest germination occurred in seed having the basal attachment scar in direct contact with the soil. He further reported that the pappus also played an important role in seed placement and germination of Leontodon autumnalis, Senecio

viscosus, S. jacobaea, and Sonchus oleraceus. The awn, which is a seed appendage, like the pappus, of Avena fatua (Thurston 1960) orients and helps bury the seed. The removal of the awn of these seeds substantially reduced germination.

The pappus can act as an anchor to prevent seed movement before and during germination and establishment of surface-seeded species. Anchoring the seed to the growth medium has been reported to be very important in seedling establishment of winterfat (Booth and Schuman 1983). Once the radicle emerges it has to penetrate the soil. If the seed is not anchored, it can and will move along the soil surface with little or no radical penetration. This can result in rapid dehydration of the radicle and/or seedling (Sheldon 1977). There is also a possibility that the pappus may absorb and hold moisture, which may assist germination. It is not known how the pappus of white rubber rabbitbrush responds to moisture. Sheldon (1977) reported three types of pappus response to moisture: remaining open, closing and opening, and collapsing.

When broadcast or drilled, white rubber rabbitbrush seed with pappus removed can end up in or on the soil in any number of positions (upright, upside down, horizontal, buried at any depth, or on the surface). Lack of seeding success could be influenced by seed cleaning (removing pappus) and seed placement. A greenhouse study was carried out to determine what effect these two factors have upon seedling establishment.

METHODS

Seed was collected in Salt Lake County, UT, in November 1983. Plump, full seeds were selected and divided into two lots. Using hand tweezers the pappus was removed from all seed (cleaned seed) in one lot (A). Care was taken to ensure that seeds were not damaged. The pappus was left on seeds (uncleaned) in the second lot (B).

Germination Study

Germination tests were conducted on four samples of 100 seed for lots A and B. Seeds were placed between moist paper and put in a refrigerator at 34-38 ^{o}F (1.1-3.3 ^{o}C). Germination counts were made every other day for 60 days. Germination was recorded when the radicle length reached 5 mm.

Emergence Study

Seed (8 per block) were planted in 12 treatments in a completely randomized block design. There were six treatments for each of lots A and B, with four replications per treatment, for a total of 32 seeds per treatment.

Planting treatments were: [1]Lot A cleaned seed (pappus removed): (1) seed vertical, crown up, half of seed out of soil; (2) seed vertical, crown up, seed crown 1-2 mm below soil surface; (3) seed vertical, basal end up, half of seed out of soil; (4) seed vertical basal end up, basal end 1-2 mm below soil surface; (5) seed horizontal and buried 1-2 mm below soil surface; (6) seed horizontal on soil surface, no covering. Lot B uncleaned seed (pappus on): (7) seed vertical, crown up, half of seed out of soil; (8) seed vertical, crown up, seed crown 1-2 mm below soil surface; (9) seed vertical, basal end up, half of seed out of soil; (10) seed vertical basal end up, basal end 1-2 mm below soil surface; (11) seed horizontal and buried 1-2 mm below soil surface; and (12) seed horizontal on soil surface, no covering. Seed were planted individually with tweezers in a 3:1 sand-perlite mix. Daily watering from below eliminated soil or seed movement. Emergence (appearance of colyedon above ground), growth, development, and establishment (production of first post-colyedon leaves) were recorded for 30 days following seeding.

Newman-Kuels' multiple means comparison test was used to determine differences between means

RESULTS

Germination

Removal of the seed pappus (cleaned seed) had no effect on germination of white rubber rabbitbrush seed. Mean percentage germination of cleaned seed was 91.1 and uncleaned seed 91.0.

Seed Cleaning Response

Significantly more seedlings from uncleaned seed than from cleaned seed were alive (with leaves) 30 days after seeding (table 1). Between cleaned and uncleaned seed there was no significant difference in the number of seeds that emerged over 30 days (table 2). However, a larger number of seedlings from cleaned seeds died or failed to develop post-cotyledon leaves (tables 1 and 3). Survival between emergence and 30 days was greater for uncleaned seed than cleaned seed (tables 1 and 2). Furthermore the greatest mortality occurred with cleaned seeds

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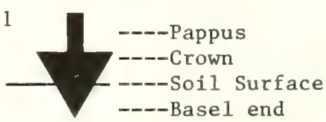
1 

that were seeded uncovered or partially covered as shown below as percent survival:

	Seed not covered or only partially covered	Seed covered
Seed with pappus	60	64
Seed without pappus	29	69

Clean seed planted on the surface or partially covered produced the greatest number of seedlings with exposed radicles. Most seedlings with bent or extended and exposed radicles died or failed to produce leaves.

Table 1.--Percentage of white rubber rabbitbrush seeds that produced live plants with at least two true leaves 30 days following seeding with various amounts of seed coverage for cleaned and uncleaned seed

Seed	Seed not covered or partially covered	Seed covered	Mean of noncovered, partially covered, and covered seed
pappus attached (uncleaned)	[1]45a	31a	38
pappus removed (cleaned)	20b	18b	19

[1]Numbers followed by the same letter are not significantly different at the 5 percent level.

Table 2.--Percentage emergence of cleaned and uncleaned white rubber rabbitbrush seed that were seeded with various amounts of covering

Seed	Seed not covered or partially covered	Seed covered	Mean of noncovered, partially covered, and covered seed
Uncleaned (pappus attached)	[1]75a	48b	61
Cleaned	70a	26b	42

[1]Numbers followed by same letter are not significantly at the 5 percent level.

Seed Placement

Seed placement had a significant effect on the number of live seedlings 30 days after seeding (tables 3A and 3B). Uncleaned seed planted upright with the crown up and basal attachment scar in contact with the soil produced the greatest number of seedlings (69 percent) (table 3A). There was no significant difference between the number of seedlings resulting from seed being covered or uncovered; however, the trend was for more seedlings from seed not covered or partially covered than from covered seed. Seedling success was significantly higher (table 3B) (41 percent success) from seeds planted upright (treatments 7, 8, 1, 2) with basal attachment scar in contact with the soil than from seeds planted horizontally (28 percent) (treatments 11, 12, 5, 6) where the basal attachment scar may have contacted the planting medium, or seeds planted upside down (17 percent) (treatments 9, 10, 4, 3) where the basal attachment scar had no soil contact (table 3B).

SUMMARY

Results from germination tests indicate the difference in seeding success was not influenced by germination, but rather by seed placement and positioning.

Uncleaned seed (pappus on) planted upright, and half buried produced the most seedlings (69 percent) of any treatment. Forty-one percent of the seeds planted upright produced seedlings with leaves, whereas only 28 percent of the seed planted horizontally and 17 percent of the seed planted upside down produced seedlings. Significantly more seedlings were produced (38 percent) from uncleaned seed than from cleaned seed (19 percent). Survival between emergence and 30 days was least (45 percent) for cleaned seed, especially those planted on the surface or partially buried (29 percent). Survival for uncleaned seed was 62 percent.

CONCLUSIONS

The pappus attached to white rubber rabbitbrush seed is generally removed to facilitate seed handling and planting. Cleaned seeds are often broadcast aerially and are thus deposited in or on the soil, in no particular position. Seedling establishment is generally very low.

Results from this study indicate that the presence or absence of the pappus does not affect laboratory germination, but does play an important role in seedling emergence and establishment. Greatest number of seedlings occurred when seeds were placed upright in or on the soil with the basal attachment scar in contact with the soil. Rabbitbrush seed are wind-dispersed and deposited; the seed pappus acts as a parachute and helps position the seed properly in the soil. The pappus can also act as an anchor, preventing movement of the seed during germination and radical penetration into the soil. Without the pappus, the seed can move along the soil surface or out of the soil exposing the radicle. Seedlings with bent and

Table 3.--Percentage of white rubber rabbitbrush seeds that produced live plants with at least two true leaves 30 days following seeding in 12 seeding treatments

A-Influenced by seed coverage

Seed not covered or partially covered		Seed covered	
Treatment	Percent	Treatment	Percent
[1]7-	[2]69a	11-	44ab
1-	44ab	8-	31bc
12-	38bc	5-	22bc
9-	9bc	2-	19bc
3-	9bc	10-	19bc
6-	6bc	4-	13bc

[1]See text footnote 1.
[2]Numbers followed by the same letter are not significantly different at the 5 percent level.

B-Influenced by seed positioning

Seed position	Percent
Seeded upright, treatments	
7- , 8- , 1- , 2-	[1]41a
Seeded horizontal, treatments	
11- , 12- , 5- , 6-	28b
Seeded upside down, treatments	
9- , 10- , 3- , 4-	17b

[1]Numbers followed by the same letter are not significantly different at 5 percent level.

exposed radicles generally do not produce healthy leaf-producing seedlings.

Uncleaned (pappus on) rabbitbrush seed is difficult to seed with most aerial or ground seeding equipment. If seeding success is to be improved, planting equipment and techniques need to be developed that will assure proper rabbitbrush seed placement.

ACKNOWLEDGMENT

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EMERGENCE, SEEDLING GROWTH, AND CRUDE TERPENOID CONCENTRATIONS IN A SAGEBRUSH GARDEN

Rick G. Kelsey

ABSTRACT: A sagebrush garden was established with seed collected from 16 populations of seven taxa in Montana. Emergence ranged from 0 to 80.5 percent. Relative seedling survival was near 74 percent or greater the first year and 90 percent or greater the second. Fertilizing the second season did not influence survival, but it doubled length, and doubled or tripled leaf biomass. Seedling crude terpenoid concentrations were lower than in parental plants and fertilizing did not affect accumulation of these compounds.

INTRODUCTION

Botanical and chemical characteristics of sagebrush indicate these shrubs have potential as a renewable source of high energy compounds and organic chemicals (Kelsey and others 1982; Kelsey, this proceedings). The epidermal surface of sagebrush leaves is covered with cuticular waxes and glandular trichomes containing monoterpenes and sesquiterpene lactones (Kelsey and Shafizadeh 1980). These hydrocarbons are readily extracted with solvents and can be removed without drying or grinding the tissue. The extract, referred to as crude terpenoids, can be converted to a high quality synthetic crude oil (biocrude) by hydrogenating (Kelsey, this proceedings).

For big sagebrush the greatest quantities of crude terpenoids have been observed in Artemisia tridentata ssp. tridentata, usually reaching 20 percent or greater of leaf dry weight, at peak concentrations in fall and winter (Kelsey and others 1982; Striby and others 1982; Personius and others unpublished data). This is also the fastest growing of the three common big sagebrush subspecies (McArthur and Welch 1982). Unlike traditional agricultural plants, species with the greatest potential for producing biocrude in arid and semiarid regions of the United States may have only low to moderate annual biomass yields (McLaughlin and others 1983).

In our studies, production of epidermal chemicals by sagebrush leaves has been shown to be independent of defoliation. In addition, partial defoliation did not adversely affect growth the following season, implying that plants could be harvested on an annual basis if clipping was not too severe (Kelsey, this proceedings). Cutting the entire crown is an alternative harvesting method that would kill the plants, except for Artemisia cana Pursh and A. tripartita Rydb. which root-sprout (Beetle 1960; McArthur and others 1979). Complete crown harvesting could b[e] used on areas where shrub eradication was the desired objective, or where shrubs could be rapidly reestablished.

Sagebrush can be readily established by transplanting seedlings from nursery stock and native stands (Plummer and others 1968; 1970; Long, thi[s] proceedings). These shrubs are prolific seed producers (Harvey 1981), and under laboratory conditions, germination can exceed 80 percent (Sabo and others 1979; Stidham and others 1980; Harvey 1981). Field germination and emergence are frequently far less (Harvey 1981). Aside from germination data, very little information i[s] available on the early growth stages of sagebrus[h] seedlings, particularly in the field. The objec[-] tive of this study was to plant a sagebrush garden from seed and measure emergence, growth, biomass productivity, and crude terpenoid concentrations of seedlings, and evaluate the results in terms of biocrude production.

MATERIALS AND METHODS

In October 1981, a garden site was selected in the Missoula valley near Fort Missoula on a Typi[c] Cryoborol soil formed in alluvial material. Elevation was 960 m. Mean annual temperature is 6.2 °C (April-October 1982, 12.9 °C; 1983, 12.4 °C) and precipitation 32.6 cm (April-October 1982, 23.0 cm; 1983, 28.1 cm) (Cordell 1971; NOA[A] 1982, 1983). Native vegetation was scraped from an 18- by 18-m area and the soil rototilled. Sixteen 3- by 3-m plots were marked, each separated by a 1 m buffer zone on all sides. A single plot was prepared for each seed source. Flower stalks were collected in November from 16 populations of seven taxa in Montana: Artemisia tridentata Nutt. ssp. tridentata (Upper Red Rock Lake, Bannack, Perma); A.t. ssp. vaseyana (Rydb.) Beetle (Reynolds Pass, Sagecreek, Lavalle Creek) A.t. ssp. vaseyana var. spiciformis (Osterh.) Beetle (Upper Red Rock Lake); A.t. ssp. wyomingensis Beetle & Young (Bannack Flats, Ramsay, Miles City Livestock and Range Research Station); A. cana Pursh ssp. cana (Sappington, Miles City Livestock and Range Research Station) A.c. ssp. viscidula (Osterh.) Beetle (Sawpit

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Creek); A. tripartita Rydb. ssp. tripartita (Monida, Badger Pass, Ovando).

Also, in one population of each taxa, three parental seed source plants were tagged and leaves sampled. Samples were sealed in Ziploc plastic bags, transported on ice to the laboratory, and stored in a freezer. They were analyzed for crude terpenoid concentrations as described by Kelsey (this proceedings). Approximately one year later, at the end of the first growing season for garden seedlings, tagged big sagebrush plants (A.t. ssp. tridentata, Perma; A.t. ssp. wyomingensis, Ramsay; A.t. ssp. vaseyana, Lavalle Creek) were sampled again and analyzed for crude terpenoid concentrations.

Dry seeds were cleaned by screening and then blowing in a commercial seed cleaner. Seed numbers were estimated by weight after accurately counting the number of seeds in 5 to 10 small weighed subsamples from each population. To help visualize dispersal, seeds were mixed with sawdust in a hand-held seeder and sown onto bare ground in late February 1982. Garden plots were randomly assigned. Number of seeds sown per plot varied considerably, from as few as 97/m^2 to 6,995/m^2 (table 1).

Seedling density was estimated in June and October 1982. Twenty-four quadrats (8 per line) were randomly positioned on 3 parallel transect lines located 0.5, 1.5, and 2.5 m from the north edge of each plot. Quadrat size (table 1) was varied between plots to accommodate the different seedling densities. In October, seedlings were collected to measure length, biomass, and crude terpenoid concentrations. Individuals were gathered from a separate set of parallel transect lines each located 0.5, 1.5, and 2.5 m from the west edge of each plot. Nine quadrats, equal to the size used for seedling counts, were positioned at 30-cm intervals along each line. Seedlings closest to the line were clipped at ground level until a desired 10 g of fresh leaf tissue was collected from the whole plot. They were sealed in Ziploc plastic bags, transported on ice to the laboratory, and stored in the freezer.

Thirty of these seedlings were randomly selected for length measurements, from the clipped stem to the tip of the longest live green leaf, when the crown was tightly pressed against a rule. For the majority of seedlings, length measurement was a close approximate of height, but on a few plots some seedlings did not stand upright. A portion of their stem laid on the soil surface before bending up to support the crown. Each successive group of 10 measured seedlings were briefly rinsed in a beaker of water to remove soil particles adhering to the leaf surface. After patting dry, the 10 seedlings were placed into an aluminum pan to air-dry. Dried seedlings were separated into leaves and stems, ovendried at 100 °C overnight, desiccated 30 minutes and weighed. Seedlings not used for length and biomass measurements remained frozen and were analyzed for crude terpenoid concentrations.

Table 1.--Emergence and relative seedling survival, for single plots, during the first growing season, 1982

Taxa[1]	Collection site	Quadrat size[2]	Seeds sown	Seedling density[3] June	Seedling density[3] October	Emergence	Relative survival
			- - - - - Number per square meter	- - - - -		- - - - Percent	- - -
Att	Red Rock Lakes	1	2,367	[4]298 ± 144	313 ± 131	12.6	105.0
Att	Perma	3	6,995	347 ± 204	[5]402 ± 218	5.0	115.9
Att	Bannack	1	2,438	316 ± 120	240 ± 136	13.0	76.0
Atw	Miles City	4	2,811	1,888 ± 1,210	1,470 ± 994	67.2	77.9
Atw	Ramsay	2	2,750	621 ± 240	583 ± 229	22.6	93.9
Atw	Bannack Flats	1	97	38 ± 33	40 ± 31	39.2	105.3
Atv	Sage Creek	1	3,348	167 ± 58	158 ± 98	5.0	94.6
Atv	Lavalle Creek	1	723	109 ± 69	140 ± 60	15.1	128.4
Atv	Reynolds Pass	1	353	0	0	0	0
Atvs	Red Rock Lakes	1	143	0	0	0	0
Acc	Sappington	3	2,936	1,884 ± 959	1,712 ± 753	64.2	90.9
Acc	Miles City	3	4,439	3,573 ± 1,279	3,094 ± 1,107	80.5	86.6
Acv	Sawpit Creek	1	1,193	111 ± 82	82 ± 71	9.3	73.9
Atptp	Ovando	1	1,422	7 ± 13	7 ± 9	0.5	100.0
Atptp	Badger Pass	1	977	4 ± 11	7 ± 13	0.4	175.0
Atptp	Monida	--	[6]0	---	---	---	---

[1]Att, Artemisia tridentata ssp. tridentata; Atw, A.t. ssp. wyomingensis; Atv, A.t. ssp. vaseyana; Atvs, A.t.v. var. spiciformis; Acc, A. cana ssp. cana; Acv, A. cana ssp. viscidula; Atptp, A. tripartita ssp. tripartita.
[2]Dimensions in centimeters, 1 = 30 by 15; 2 = 17.5 by 15; 3 = 12 by 7.3; 4 = 9.5 by 7.3.
[3]Seedling densities were not significantly different between June and October on any plot.
[4]± Standard deviation.
[5]Plot damaged and soil disturbed in spots by mole activity.
[6]Floral stalks were collected at this site but the heads contained no seed.

In March 1983, before spring growth had begun, each plot was subdivided by digging a 4-6 cm wide trench through the center. The west one-half then received 260.7 g of commercial lawn fertilizer (29-3-3, N-P-K). This was equivalent to 168 kg of nitrogen per hectare used by Bayoumi and Smith (1976). The east one-half of each plot was untreated. Seedling density was estimated in June 1983, by the same procedure used in 1982, except that along each line four quadrats were randomly positioned in the fertilized side and four in the unfertilized side. Also, two seedlings closest to the transect line in each quadrat were measured for height. Final seedling counts were made in late October (eight plots) and early November (three plots) 1983, referred to as October for the purpose of discussion. Quadrat sampling was the same as in June, but all seedlings in the quadrats were clipped at ground level and handled as described above. Length, leaf biomass, and crude terpenoid concentrations were determined as in 1982, except rinsing soil from leaves was unnecessary. After quadrat sampling was completed, additional seedlings were collected in November and combined with the quadrat seedlings for analysis of crude terpenoid concentrations.

Grasses and forbs germinated and grew on all plots, but not in great densities the first year. Spotted knapweed (Centaurea maculosa Lam.) was one of the most abundant and serious competitors. To estimate competition from knapweed during 1983, all plants (including those in a rosette stage) were counted in each quadrat and clipped at ground level in October-November 1983. Clippings were put into paper bags, ovendried 24 hours at 60 °C, adjusted to room temperature for a minimum of 30 minutes, and then weighed.

Seedling length and leaf biomass were compared for fertilized and unfertilized subplots of each seed source using the Student t-test. Seedling densities (June vs. October in 1982 and 1983) were analyzed by the Student t-test for paired comparisons, at the 0.05 level of probability. Product-moment correlation coefficients were calculated to determine relationships between seedling densities and total seedling biomass 1982, leaf biomass 1983, and plant length 1982, 1983 (Sokal and Rohlf 1981).

RESULTS

Large quantities of seed were sown, when available, to compensate for the poor emergence and survival reported by Harvey (1981). Emergence was variable, ranging from 0 to 80.5 percent (table 1). Artemisia tridentata ssp. vaseyana and A. tripartita ssp. tripartita were poorest and A. cana ssp. cana the best, followed by A. tridentata ssp. wyomingensis (table 2). Habitat characteristics of the latter two taxa were the most different from those at the garden site (an A.t. ssp. vaseyana habitat). Miles City seeds, the best performers, were collected the greatest distance from the garden. Emergence was not complete on some plots the first week in June, as indicated by an increased seedling density in October. June is normally the wettest month in the Missoula valley (Cordell 1971), and conditions are ideal for sagebrush germination. Late germination and emergence replaced seedlings that died, making it difficult to measure survival accurately. This may explain why summer survival was extremely high, 74 percent or greater on every plot (tables 1 and 2). Consequently, these values should be considered as relative survival. There was no significant difference in seedling densities between June and October (table 1) on any plot.

Table 2.--Emergence, relative survival, length, and biomass, by taxa, the first growing season, 1982

Taxa[1]	Emergence	Relative survival	Length	Total seedling biomass	Leaf biomass
	- - Percent - -		Millimeters	Milligrams dry weight per 10 seedlings	
Att(3)	10.2	99.0	29	244	159
Atw(3)	43.0	92.4	25	175	109
Atv(2)	6.7	111.5	32	325	209
Atvs(1)	0.0	---	--	---	---
Acc(2)	72.4	88.8	35	226	136
Acv(1)	9.3	73.9	26	242	154
Atptp(1)	0.5	137.5	[2]--	[2]---	---

[1]Abbreviations same as table 1. Number of plots averaged in parentheses.

[2]These were not sampled because of the small seedling number.

At the end of the first growing season, seedling length ranged from 23 mm for A. tridentata ssp. wyomingensis from Bannack Flats to 39 mm for A.t. ssp. vaseyana from Lavalle Creek (table 3). Although seedlings of the latter taxa were tallest based on plots, A. cana ssp. cana seedlings were tallest based on taxa (table 2). High seedling densities did not influence plant size. There was no correlation between October densities (table 1) and seedling length (r^2 = 0.21) or biomass (r^2 = 0.02).

Seedling biomass of A.t. ssp. vaseyana was greatest, largely a result of the Lavalle Creek plot from seeds collected locally near Missoula (tables 2 and 3). Biomass of A.c. ssp. cana was less than A.t. ssp. vaseyana because of greater leaf senescence and loss. As expected, short A.t. ssp. wyomingensis produced the least dry matter.

Seedling crude terpenoid concentrations were low relative to parental plants collected the previous year (table 4) and compared to three parental populations resampled after clipping the garden seedlings in early November 1982. Mature shrubs in their natural habitats produced approximately twice the concentrations of crude terpenoids (table 4).

Table 3.--Seedling length and biomass, for single plots, at the end of the first growing season, October 1982

Taxa[1]	Collection site	Length	Total seedling biomass	Leaf biomass
		Millimeters	- - - Milligrams dry weight per 10 seedlings - - -	
Att	Red Rock Lakes	[2]27 ± 9	198 ± 26	129 ± 15
Att	Perma	31 ± 12	247 ± 156	160 ± 94
Att	Bannack	30 ± 10	287 ± 125	188 ± 84
Atw	Miles City	26 ± 9	195 ± 38	122 ± 29
Atw	Ramsay	25 ± 6	157 ± 31	96 ± 18
Atw	Bannack Flats	23 ± 6	173 ± 42	108 ± 22
Atv	Sage Creek	24 ± 9	228 ± 49	164 ± 35
Atv	Lavalle Creek	39 ± 1	422 ± 33	254 ± 11
Atv	Reynolds Pass	---	---	---
Atvs	Red Rock Lakes	---	---	---
Acc	Sappington	32 ± 10	193 ± 31	113 ± 18
Acc	Miles City	37 ± 12	258 ± 79	158 ± 54
Acv	Sawpit Creek	26 ± 10	242 ± 32	154 ± 25
Atptp	Ovando	[3]---	[3]---	[3]---
Atptp	Badger Pass	[3]---	[3]---	[3]---
Atptp	Monida	---	---	---

[1]Abbreviations same as table 1.
[2]± Standard deviation.
[3]These were not sampled because of the small seedling number.

Table 4.--Crude terpenoid concentrations in parental populations (1981, 1982) and garden seedlings (1982, 1983)

Taxa[1]	Collection site	Parental plants[2]		Garden seedlings[3]		
		1981	1982	1982	1983 unfertilized	1983 fertilized
		- - - - - - - - - - - - - Percent leaf dry weight - - - - - - - - - - - - -				
Att	Red Rock Lakes	---	---	8.4	11.6	12.9
Att	Perma	[4]22.9 ± 3.3	24.6 ± 3.0	12.4	15.3	18.6
Att	Bannack	---	---	10.7	13.5	13.6
Atw	Miles City	---	---	15.0	15.1	14.1
Atw	Ramsay	18.1 ± 2.1	19.7 ± 3.3	9.5	11.4	11.0
Atv	Sage Creek	---	---	8.0	9.5	9.0
Atv	Lavalle Creek	11.3 ± 0.6	15.1 ± 1.1	7.0	10.1	9.6
Atvs	Red Rock Lakes	13.9 ± 0.9	---	---	---	---
Acc	Sappington	16.2 ± 7.5	---	9.3	10.2	10.7
Acc	Miles City	---	---	10.2	11.5	9.2
Acv	Sawpit Creek	8.2 ± 0.9	---	2.2	---	---
Atptp	Ovando	18.2 ± 3.5	---	---	---	---

[1]Abbreviations same as table 1.
[2]An average of three plants per collection site, 1982 plants were the same as 1981.
[3]Duplicate analysis per collection except six sites in 1982 with limited leaf material.
[4]± Standard deviation.

Relative seedling survival through the second summer was excellent (tables 5 and 6), averaging 90 percent or greater (table 6) for all taxa except fertilized A. cana ssp. viscidula. Seedling densities were not significantly different between June and October, although densities on several plots were greater in October. Some of this increase could have been due to variation and/or sampling error, and some probably resulted from residual seed in the soil that emerged after June sampling, since increases were observed mainly on plots sown with 2,000 or more seeds/m^2 (tables 1 and 5). Conditions during June and July 1983 were excellent for germination, with lower than average temperatures and above normal precipitation (NOAA 1983). The largest increases in seedling numbers were observed on A. cana plots (table 5) where lateral

Table 5.--Relative seedling survival, for single plots, during the second growing season, 1983

Taxa[1]	Collection site	Treatment[1]	Seedling density[2] June	Seedling density[2] October	Relative survival	Establishment[3]
			- -Number per square meter- -		- - - - - Percent - - - - -	
Att	Red Rock Lakes	F	[4]262 ± 136	280 ± 164[a]	106.9	11.8
		C	231 ± 169	227 ± 127[a]	98.3	9.6
Att	Perma	F	[5]287 ± 198	[5]191 ± 191[a]	66.6	2.7
		C	171 ± 129	171 ± 151[a]	100.0	2.4
Att	Bannack	F	[5]164 ± 111	[5]162 ± 93[a]	98.8	6.6
		C	198 ± 167	[6]200 ± 167[a]	101.0	8.2
Atw	Miles City	F	1,311 ± 591	1,527 ± 908[a]	116.5	54.3
		C	1,225 ± 562	1,282 ± 980[a]	104.7	45.6
Atw	Ramsay	F	495 ± 103	488 ± 114[a]	98.6	17.8
		C	510 ± 190	423 ± 164[a]	82.9	15.4
Atw	Bannack Flats	F	29 ± 27	[7]16 ± 22[a]	55.2	16.4
		C	29 ± 29	27 ± 20[a]	93.1	27.7
Atv	Sage Creek	F	151 ± 69	133 ± 60[a]	88.1	4.0
		C	140 ± 56	167 ± 96[a]	119.3	5.0
Atv	Lavalle Creek	F	122 ± 40	[7]129 ± 56[a]	105.7	17.8
		C	84 ± 49	71 ± 51[b]	84.5	9.8
Acc	Sappington	F	1,667 ± 947	1,747 ± 776[a]	104.8	59.5
		C	1,598 ± 811	1,884 ± 1,244[a]	117.9	64.2
Acc	Miles City	F	2,785 ± 1,244	[7]3,436 ± 1,153[a]	123.4	77.4
		C	2,534 ± 1,221	3,059 ± 1,233[a]	120.7	68.9
Acv	Sawpit Creek	F	89 ± 47	[7]51 ± 44[a]	57.3	4.3
		C	64 ± 53	78 ± 56[a]	121.9	6.5
Atptp[8]	Badger Pass	F	18 ± 27	[9]---	---	---
		C	13 ± 16	---	---	---

[1]Abbreviations same as table 1. Treatment, F = fertilized; C = control.
[2]Seedling densities were not significantly different between June and October on any plot. When fertilize and control of the same plot are followed by different letters, they are significantly different (p <0.05
[3]Number of seedlings in October 1983 as a percentage of the number of seeds sown in February 1982.
[4]± Standard deviation.
[5]Soils on the fertilized half of this plot were heavily disturbed by mole activity, burying and killing seedlings in some spots.
[6]Moderate mole damage.
[7]Some plot damage from mouse trails.
[8]The Ovando Atptp plot was vandalized during the winter and could not be used.
[9]Not sampled.

Table 6.--Relative seedling survival, establishment, length, and leaf biomass, by taxa, at the end of the second growing season, 1983

Taxa[1]	Treatment[1]	Relative survival	Establishment	Length	Leaf biomass
		- - Percent	- -	Millimeters	Milligrams dry weight per 10 seedlings
Att(3)	F	90.8	7.0	73	445
	C	99.8	6.7	40	250
Atw(3)	F	90.1	29.5	66	301
	C	93.6	29.6	28	100
Atv(2)	F	96.9	10.9	93	485
	C	101.9	7.4	36	267
Acc(2)	F	114.1	68.5	66	234
	C	119.3	66.6	39	79
Acv(1)	F	57.3	4.3	78	217
	C	121.9	6.5	34	166

[1]Abbreviations same as table 1. Number of plots averaged in parentheses. Treatment, F = fertilized; C = control.

branching below soil level, or vegetative sprouts from existing seedlings, may have contributed to the higher counts (Walton, personal communication).

Seedling density was similar on fertilized and unfertilized plots in June and October (except for A.t. ssp. vaseyana from Lavalle Creek in October, table 5). However, fertilization resulted in increased productivity of grasses and forbs, particularly knapweed (table 7). Visual observations suggested competition was more severe on the fertilized portion of each plot. High shrub densities did not increase seedling mortality (table 5). Moderate to heavy soil disturbances from mole activity occurred in two A.t. ssp. tridentata plots and may have reduced seedling numbers of the Perma collection (table 5). Mouse trails were observed on several fertilized subplots, but mice had minimal impact on the young seedlings.

Table 7.--Knapweed density and biomass on the sagebrush seed plots, October 1983

Taxa[1]	Collection site	Treatment[1]	Knapweed Plants (Number per square meter)	Knapweed Biomass (Grams dry weight per square meter)
Att	Red Rock Lakes	F	140 ± 56	271 ± 174
		C	140 ± 78	168 ± 97
Att	Perma	F	80 ± 58	175 ± 179
		C	76 ± 29	202 ± 111
Att	Bannack	F	82 ± 56	177 ± 155
		C	84 ± 44	116 ± 101
Atw	Miles City	F	130 ± 144	332 ± 388
		C	130 ± 115	126 ± 102
Atw	Ramsay	F	130 ± 69	384 ± 246
		C	160 ± 91	200 ± 133
Atw	Bannack Flats	F	96 ± 58	260 ± 198
		C	116 ± 42	168 ± 87
Atv	Sage Creek	F	109 ± 49	265 ± 150
		C	84 ± 44	168 ± 80
Atv	Lavalle Creek	F	193 ± 89	382 ± 203
		C	158 ± 58	236 ± 58
Acc	Sappington	F	194 ± 160	473 ± 394
		C	126 ± 137	347 ± 189
Acc	Miles City	F	69 ± 80	230 ± 112
		C	171 ± 137	245 ± 164
Acv	Sawpit Creek	F	196 ± 124	336 ± 169
		C	111 ± 51	150 ± 103

[1]Abbreviations same as table 1. Treatment, F = fertilized; C = control.

Fertilized seedling were significantly taller (1.5-2.7 times) than controls on all plots in October (table 8) as indicated by their length measurements. Length, however, was not correlated ($r^2 = 0.04$) with seedling density. Fertilized (table 6) A. tridentata ssp. vaseyana seedlings were tallest, followed by A. cana ssp. viscidula and A. tridentata ssp. tridentata (this taxon did have one plot with plants taller than the A.c. ssp. viscidula, table 8.) Without fertilization, A.t. ssp. tridentata seedlings were tallest, A.c. ssp. cana second, and A.t. ssp. vaseyana a close third. Seedlings of A.t. ssp. wyomingensis were shortest (except the Miles City fertilized plot) regardless of treatment. Artemisia cana ssp. cana seedlings were also short when fertilized (table 6), because of their deciduous nature. Seedling length on unfertilized subplots, in October 1983, had increased very little from the previous year (tables 3 and 8) indicating nutrient unavailability was limiting growth.

Leaf biomass of fertilized plants was 1.3 to 3.2 times greater than that of unfertilized controls (tables 6 and 8). Leaves were noticeably larger on fertilized seedlings. Fertilized A.t. ssp. tridentata from Bannack produced the most biomass per plot, but A.t. ssp. vaseyana produced the most biomass per taxa. This same relationship was observed for unfertilized seedlings. The

Table 8.--Seedling height (June), length (October) and leaf biomass (October), for single plots, at the end of the second growing season, 1983

Taxa[1]	Collection site	Treatment[1]	June height (Millimeters)	October[2] length (Millimeters)	Leaf biomass[2] (Milligrams dry weight per 10 seedlings)
Att	Red Rock Lakes	F	[3]80 ± 39	68 ± 26a	336 ± 100a
		C	38 ± 22	32 ± 10b	159 ± 39b
Att	Perma	F	62 ± 30	66 ± 29a	372 ± 67a
		C	28 ± 13	43 ± 16b	178 ± 26b
Att	Bannack	F	91 ± 36	84 ± 31a	628 ± 80a
		C	40 ± 22	45 ± 15b	414 ± 37b
Atw	Miles City	F	64 ± 24	73 ± 33a	300 ± 135a
		C	32 ± 9	32 ± 10b	104 ± 14a
Atw	Ramsay	F	61 ± 19	62 ± 28a	302 ± 38a
		C	24 ± 7	26 ± 6b	95 ± 16b
Atw	Bannack Flats	F	66 ± 25	62 ± 15a	---
		C	30 ± 12	27 ± 9b	---
Atv	Sage Creek	F	86 ± 38	85 ± 31a	541 ± 84a
		C	29 ± 13	32 ± 9b	328 ± 104a
Atv	Lavalle Creek	F	107 ± 42	100 ± 34a	429 ± 16a
		C	41 ± 11	40 ± 10b	205 ± 58b
Acc	Sappington	F	67 ± 28	66 ± 20a	218 ± 88a
		C	42 ± 14	38 ± 11b	82 ± 16a
Acc	Miles City	F	71 ± 20	66 ± 16a	249 ± 34a
		C	41 ± 13	40 ± 10b	76 ± 14b
Acv	Sawpit Creek	F	80 ± 38	78 ± 36a	217 ± 124a
		C	38 ± 11	34 ± 12b	166 ± 35a
Atptp[4]	Badger Pass	F	71 ± 32	[5]---	[5]---
		C	27 ± 8	---	---

[1]Abbreviations same as table 1. Treatment, F = fertilized; C = control.
[2]When fertilized and control of the same plot are followed by different letters, they are significantly different ($p < 0.05$).
[3]± Standard deviation.
[4]The Ovando Atptp plot was vandalized during the winter and could not be used.
[5]Not sampled because of small seedling numbers.

smallest leaf biomass in October was collected from subspecies of A. cana (except untreated A.c. ssp. viscidula). This is somewhat misleading because A. cana has more foliage earlier in the growing season, but is nearly deciduous, losing a greater portion of its leaves than big sagebrush subspecies. Fertilizing doubled or tripled leaf dry matter productivity for over two-thirds of the taxa (tables 6 and 8). Foliage biomass was not correlated ($r^2 = 0.32$) with seedling density in October. Some unfertilized seedlings had less leaf dry weight in 1983 than they did in 1982 (tables 2,3,6, and 8).

Crude terpenoid concentrations were not affected by fertilization (table 4). Concentrations in October 1983 were greater than one year earlier, but they were still lower than those recorded for mature parental plants in their natural populations, from the previous two years.

DISCUSSION

As expected from other studies (Harvey 1981; McArthur and Welch 1982) the emergence and growth of sagebrush, under uniform environmental conditions, varied considerably between taxa, within taxa from different geographic sources, and between individuals originating from the same population.

These results have important implications in terms of utilizing sagebrush species as biocrude producing plants. Undoubtedly, it would not be possible to grow an annually harvested crop of sagebrush plants from seed, even if plants were provided with ideal conditions. Sagebrush simply does not grow fast enough. However, since the shrubs can be partially defoliated without damaging growth (Kelsey, this proceedings), there would be no need to start from seed each year. Establishment from seed could still be important for sites that required complete shrub harvesting at periodic intervals, or where existing sagebrush plants were removed for replacement with a more productive form. Since sagebrush can be readily transplanted (Plummer and others 1968, 1970), nursery stock could be grown in gardens or in greenhouses (Long, this proceedings). Sagebrush seed is one of the least expensive to collect relative to other western shrubs (Plummer and others 1968).

The good germination and growth of A. cana ssp. cana, particularly those from Miles City, show that a variety of taxa can be grown on a given site. Successful establishment of various taxa was partially the result of favorable weather conditions during the study period and other beneficial environmental characteristics of this particular habitat. The same taxa may have responded differently in other environments or weather conditions.

Artemisia cana ssp. cana and A. tripartita ssp. tripartita might be more desirable than A. tridentata for biocrude production because they root-sprout (Beetle 1960; White and Currie 1983). The crude terpenoid concentrations in these two taxa were higher than in A. tridentata ssp. vaseyana (table 4). Further studies of A. cana would be necessary to determine optimal harvest time because of its deciduous nature.

Seedling growth responded quite positively to the application of fertilizer (tables 6 and 8), but there was no change in crude terpenoid concentrations. A similar growth response was observed when mature sagebrush was fertilized (Bayoumi and Smith 1976). For many plants, an inverse relationship exists between growth and chemical concentrations (McLaughlin and Hoffmann 1982; McLaughlin and others 1983). Various types of compounds, i.e., terpenes, lipids, and hydrocarbons, accumulate in plants subjected to stresses such as lack of water, insufficient nutrients, or herbivory (Bryant 1981). In sagebrush, the accumulation of epidermal compounds appears independent of stress associated with moderate to heavy defoliation (Kelsey, this proceedings), or growth stimulated by fertilization (this study). Consequently, increasing biomass production of these shrubs, by optimizing growing conditions, would directly increase the yield of epidermal chemicals from the plant, but without changing concentrations. Faster growing strains, or taxa, could be used to replace less productive populations.

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GERMINATION PROFILES FOR FIVE POPULATIONS OF BIG SAGEBRUSH

Raymond A. Evans and James A. Young

ABSTRACT: Seeds from two sources of mountain big sagebrush (Artemisia tridentata Nutt. ssp. vaseyana [Rydberg] Beetle), and three sources of basin big sagebrush (A. tridentata Nutt. ssp. tridentata) were tested from collections made in the same stands in 2 consecutive years. Germination tests were conducted at 55 constant and alternating temperatures. Basin big sagebrush seeds had higher germination at several categories of temperatures than seeds of mountain big sagebrush.

INTRODUCTION

The potential of seeds to germinate at various constant and alternating temperatures is one of the basic parameters governing the periodicity of germination and establishment of plants in wildland seedbeds. Obviously, temperature interacts with other microenvironmental parameters, such as moisture availability and seedbed soil conditions. However, determining germination-temperature response provides an important start toward understanding the complex interactions that affect germination. This study was undertaken to determine germination of big sagebrush seeds in relation to 55 different constant and alternating temperatures.

METHODS

Seeds of big sagebrush were collected in November 1982 and 1983 at five sites in western Nevada where reciprocal gardens of big sagebrush plants were located. The sites ranged from low-elevation (1 500 m) sagebrush communities, adjacent to the salt desert, to the lower fringes of the pinyon/juniper (Pinus/Juniperus) woodlands at 1 800 m elevation. Precipitation on the sites varied from 150 mm to 300 mm. Granite Peak and Churchill Canyon site #5 supported mountain big sagebrush and the other three sites, basin big sagebrush. Seeds were collected from natural stands, allowed to dry to moisture equilibrium, hand threshed, and cleaned with an air screen.

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Seeds were stored in paper bags in the laboratory until tested. Tests were conducted 30 days, 6 months, and 12 months after harvest.

In all germination tests, four replications of 25 seeds each were used. Tests were conducted in petri dishes with the seeds placed on top of one thickness of germination paper and moistened with tap water.

Tests were conducted in dark germinators for 4 weeks with germination counts made weekly. Unless otherwise specified, seeds were considered germinated when the radicle emerged (0.25 cm).

Constant temperatures used were 0, 2, 5, 10, 15, 20, 25, 30, 35, and 40 °C. Alternating temperature regimes consisted of 16 hours at each lower constant temperature (cold period) and 8 hours at all possible higher temperatures (warm period) in each 24-hour period. For example, 0 was alternated with 2, 5, 20, 15, 20, 25, 30, 35, and 40 °C, whereas 35 was alternated with 40 °C only.

The effects of constant alternating temperatures on percentage germination were statistically analyzed using a quadratic response surface (Ott 1977). A quadratic response surface was developed for each cultivar or accession using multiple regression techniques. Estimated germination values and their confidence limits were derived from the quadratic response surface of each species for each cold-period (16 hours) temperature through the series of warm-period (8 hours) temperatures (Evans and others 1982). The generalized quadratic equation used in calculating expected values was:

$$Y = A_0 + A_1X_1 + A_2X_2 + A_3X_1 + A_4X_2 + A_5X_1X_2$$

where Y = percent predicted germination, A_0 = intercept, A_1 through A_5 = coefficients, X_1 = cold temperature, and X_2 = warm temperature. The intercept and coefficients were determined by multiple regression for individual species. The resulting values for A_1 through A_5 represent partial regression coefficients where the effect of one variable on germination is altered by the inclusion of the remaining variables. Calculated regression lines with confidence limits were compared with actual seed germination data.

We compared the germination percentage of the seeds tested at constant and alternating

temperatures with categories of seedbed temperatures that were developed on the basis of microenvironmental monitoring in the field (Evans and others 1970; Evans and Young 1970, 1972). These temperature categories were:

Very cold: 0, 0/2, 2, and 0/5 °C.

Cold: 0/10, 0/15, 2/5, 2/10, 2/15, 5/15, and 5/10 °C.

Cold fluctuating: 0/20 through 0/40 °C, 2/20 through 2/40 °C.

Moderate: 5/15 through 5/25 °C; 10 through 10/30 °C; 15 through 15/35 °C; 20 through 20/35 °C; 25 and 25/30 °C.

Fluctuating: 5/30, 5/35, 5/40, 10/35, 10/40, and 15/40 °C.

Warmer: 20/40, 25/35, 25/40, 30, 30/35, 30/40, 35, 35/40, and 40 °C.

A series of germination profile characteristics was generated from the response surfaces: (a) mean germination, (b) mean germination in the regimes producing some germination, (c) percentage of regimes with some germination, (d) percentage of regimes with optimum germination, (e) mean of germination optima, and (f) maximum germination (Young and Evans 1982). We define optimum germination as that equal to or greater than the maximum mean germination minus one-half its confidence interval (P=0.01).

RESULTS AND DISCUSSION

Variation Between Years

There was no significant (P=0.05) difference between the average germination for the seeds of big sagebrush produced at each location between 1982 and 1983 (table 1). Based on previous experience, we find it unusual that seeds from the same parents in different production years do not have marked differences. Generally, year-to-year variations in environmental conditions will have a big influence on seed germination.

Differences Among Locations

For this presentation, we averaged profiles for the 2 years and present mean germination parameters (table 2). Seeds produced at Churchill Canyon #1 and #3 had higher average germination at the 55 constant and alternating temperatures (table 2). Both of these locations support basin big sagebrush communities. Seeds from the other basin big sagebrush location, Medell Flat, and the mountain big sagebrush community at Churchill Canyon #5 were intermediate in germination. Seeds from the remaining mountain big sagebrush community at Granite Peak were significantly (P=0.01) lower in germination.

For certain species, germination may occur at only a few temperature regimes, but be very high at those restricted temperatures. This was not the case for the seeds used in this study. The germination mean of temperature regimes with some germination was very similar to the overall mean germination (table 2). Germination occurred at more than 90 percent of the temperatures tested; only the highest temperature regimes failed to produce germination. Optimum germination occurred in 12 to 19 percent of the temperature regimes tested (table 2). Maximum germination and germination at optimum temperatures were quite high except for the seeds of mountain big sagebrush produced at Granite Peak.

Distribution of Optimum Temperatures

Only two temperature regimes, 10/20 °C and 15/20 °C, were always optimum for seed germination (table 3). The range of temperature regimes that supported optimum germination at least once was quite wide, encompassing 19 regimes or 35 percent of those tested. Seeds of mountain big sagebrush produced at Granite Peak had the widest range of optima and those of the same subspecies produced at the Churchill Canyon #5 location had the narrowest, 29 and 9 percent of all regimes tested, respectively.

Cool-Moist Stratification Requirements

McDonough and Harniss (1974) reported that seeds of mountain big sagebrush collected in Idaho had

Table 1.--Mean germination of optima, and maximum germination for big sagebrush seeds produced at five locations in 1982 and 1983

	Year of seed production					
	Mean germination		Mean of optima		Maximum germination	
Location	1982	1983	1982	1983	1982	1983
	- - - -	- - - -	- - - -	percent - - - -	- - - -	- - - -
Granite Peak	34	35	59	55	63	57
Medell Flat	51	59	78	89	81	92
Churchill Canyon #1	59	69	84	93	87	95
Churchill Canyon #3	71	69	93	91	95	93
Churchill Canyon #5	48	46	82	75	86	79

Table 2.--Germination parameters synthesized from quadratic response surfaces for germination at 55 constant and alternating temperatures for five sources of seeds of big sagebrush. Figures are means for seeds produced at the same site in 1982 and 1983[1]

Germination parameter	Locations: Granite Peak	Medell Flat	Churchill Canyon #1	Churchill Canyon #3	Churchill Canyon #5
	- - - - - - -	- - - - - - -	percent	- - - - - - -	- - - - - - -
Mean germination	34c	55b	69a	70a	47b
Mean germination of regimes with some germination	36	57	66	72	51
Regimes with some germination	96	97	97	98	93
Regimes with optimum germination	19	12	17	15	15
Mean of optima	57	84	89	92	79
Maximum germination	60	87	91	94	82

[1]Means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

Table 3.--Frequency of temperature regimes that supported optimum germination in quadratic response surfaces based on 55 constant and alternating temperatures. Seeds of big sagebrush from five locations produced in 1982 and 1983 used for a total of 10 response surfaces

Cold period temperature-16 hours, °C	Warm period temperature - 8 hours °C: 0	2	5	10	15	20	25	30	35	40
0				10	10					
2				10	10	20				
5				20	30	10				
10			10	40	100	80	40			
15				40	100	90	60			
20					60	60				
25										
35										
40										

enhanced germination following cool-moist stratification at 0 to 2 °C for 30 days. The temperature regimes and the duration of incubation used in this study essentially produced self-stratifying incubation conditions. We have subjected seeds from all five sources to cool-moist stratification enrichment with potassium nitrate or gibberellin as substitutes for stratification requirements without enhancing germination above that obtained with a nonpretreated profile (Evans and Young, unpublished data).

Relating Temperature Profiles to Seedbed Temperatures

At moderate seedbed temperatures, the same pattern in regard to mean germination in relation to location was apparent that existed for overall mean germination (table 4). Seeds from Churchill Canyon #5 and Medell Flat were intermediate, and seeds from Granite Peak were markedly lower.

The germination of seeds from all sources was significantly (P=0.05) lower at very cold compared to moderate temperatures (table 4). However, the relative percentage decrease was less for mountain big sagebrush than for basin big sagebrush seeds (table 4). At cold seedbed temperatures, germination of Granite Peak mountain big sagebrush was 98 percent of what it was at moderate seedbed temperatures. The average germination of basin big sagebrush sources was 26 percent lower than that observed at moderate seedbed temperatures.

Germination of cold-fluctuating seedbed temperatures is an important category because the small seeds of big sagebrush are normally dispersed to the soil surface where they are exposed to widely fluctuating temperatures during germination. High incubation temperatures tend to depress germination of both mountain and basin big sagebrush seeds for the sources tested (table 4). This depression is roughly equal for the two subspecies, 67 percent for mountain and 65 percent for basin big sagebrush. However, under cold-fluctuating incubation regimes (combination of warmer and very cold temperatures), there is a disproportionate depression in germination of the mountain big sagebrush seeds. Compared to moderate temperatures, the cold-fluctuating regimes depressed the germination of the mountain big sagebrush sources 40 percent and of the basin big sagebrush seeds only 27 percent (table 4).

able 4.--Germination of seeds from five sources of big sagebrush at categories of seedbed temperatures based on monitoring of seedbed environments in the field. Data represent the mean for seeds produced in 1982 and 1983[1]

ategories of seedbed emperatures	Granite Peak	Medell Flat	Churchill Canyon #1	Churchill Canyon #3	Churchill Canyon #5
	percent				
oderate	48 fg	75 a-c	83 a	86a	69 b-d
ery cold	33 ik	25 kl	32 j-l	41 hi	28 j-l
old	47 gh	57 ef	57 ef	65 c-3	53 fg
old fluctuating	31 j-l	53 fg	66 c-e	80 ab	39 bi
luctuating	24 k-m	44 g-i	76 a-c	76 a-c	59 d-f
armer	13 m	21 lm	30 i-l	36 h-j	27 j-l

Means followed by the same letter are not significantly different at the 0.05 level of probability as etermined by Duncan's multiple range test.

elation to Establishment from Direct Seeding in ield

'or all locations and seasons of seeding, where irect seeding resulted in seedling establishment, eeds of mountain big sagebrush outperformed seeds f basin big sagebrush (Young and Evans, this roceedings). The results of seeding reciprocal ardens in the field appear to be opposite of what he results of the temperature profiles suggest. everal factors have to be considered in nterpreting the results.

'irst, the field data are based on emergence nd/or persistence of seedlings compared to radicle mergence in the laboratory data. These different lata bases allow the introduction of unaccountable ariables. One of the most important of these may e the susceptibility of big sagebrush seedlings o injury by frost. Seeds of most cultivars of lfalfa (Medicago sativa L.) have excellent ermination even at slightly subfreezing temperatures, but the seedlings are very susceptible to frost injury (Young and Evans, unpublished data).

The percentage of mountain big sagebrush seed emergence in the field often neared the optimum germination percentages for these seeds in laboratory tests. Either the potential of spring seedbeds to support germination is greater than we have evaluated, or some factor enhances mountain big sagebrush seed germination in the field compared to in the laboratory.

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SEEDLING ESTABLISHMENT OF FIVE SOURCES OF BIG SAGEBRUSH IN RECIPROCAL GARDENS

James A. Young and Raymond A. Evans

ABSTRACT: Establishment rates of five populations of big sagebrush (Artemisia tridentata Nutt.) by direct seeding and transplantings were investigated in five reciprocal gardens. Seeds (achenes) of mountain big sagebrush (A. tridentata ssp. vaseyana [Rydberg] Beetle) had the highest germination and establishment even on basin big sagebrush (A. tridentata Nutt.) sites. There were large differences in establishment of big sagebrush by direct seeding between years and among collections and sites. Initial results indicated that mountain big sagebrush plants were more vigorous than basin big sagebrush.

INTRODUCTION

Reciprocal gardens constitute a valuable research concept for the partitioning of phenotypic from inherent variability in populations of native plants. The potential of this concept was illustrated by the classic study by Clausen and others (1948).

The division of big sagebrush (Artemisia tridentata Nutt.) into subspecies that occupy relatively distinct ecological sites provided a suitable species for application of the concept of reciprocal gardens (Beetle 1960; Beetle and Young 1965; Winward and Tisdale 1977).

Our purpose was to study the establishment from seed and transplants of five populations of big sagebrush grown in reciprocal gardens in Nevada.

METHODS

Seeds (achenes) were collected from big sagebrush populations growing on five different sites in western Nevada in 1982 (table 1). The collection and garden sites ranged from the 1 460-m elevation sagebrush communities adjacent to chenopod desert communities, to the lower fringes of the pinyon-juniper (Pinus/Juniperus) woodlands at 1 830 m. The sites were located in the first mountain ranges east of the Sierra Nevada Mountains, within 160 km of Reno, NV. The soils at Granite Peak and Medell Flat locations are derived from decomposing granite or quartz diorite. The soils of Churchill Canyon are developed on alluvium from volcanic and metavolcanic sources.

Direct Seeding Experiments

During December 1982, corresponding to the time of natural seed dispersal, we seeded in pots 100 seeds of sagebrush from each of the five populations. The 15-cm diameter pots were filled with soil from each location and buried to the soil surface. The burial sites at each of the five locations were in areas cleared of all vegetation. A randomized block design was used with six replications. Seeds were sprinkled on the soil surface, then left uncovered.

As soon as seedlings were noted, we counted the number of living seedlings per pot on a weekly basis. At the same time, the number of naturally occurring big sagebrush seedlings in the surrounding plant community was estimated by counting seedlings in 100 randomly located quadrats 0.01 m^2 in area. Direct seeding was repeated in March and December 1983, and March 1984.

In an additional six-replicated experiment established during December 1983, we filled two sets of pots for burying at each location with a sandy loam-textured soil that had been dried and screened for use in greenhouse planting. The pots were filled and watered repeatedly until the soil was compacted and nearly level. At each location, one set of these pots was seeded by sprinkling seeds from each of the five populations on the soil surface as in the original experiments. The second set of pots had 20 colored glass marbles 1.25 cm in diameter placed on the soil surface before seeding. The marbles covering the soil surface prevented rapid evaporation from the soil surface and provided a more favorable microenvironment for seed germination and seedling growth.

Transplant Experiments

Seeds collected from each location in December 1982 were used to grow seedlings in 15-cm plots in the greenhouse. The seedlings were transplanted to the gardens in May 1983. The

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Table 1.--Characteristics of the five plant communities where Artemisia tridentata seeds were collected and reciprocal gardens located

Location	Elevation (m)	Artemisia tridentata subspecies	Soils	Estimated annual precipitation (cm)
Granite Peak	1830	vaseyana	Typic Haplargids	30
Churchill Canyon #5	1830	vaseyana	Typic Argixerolls	30
Churchill Canyon #3	1690	tridentata	Typic Torripsammonts	25
Churchill Canyon #1	1460	tridentata	Typic Torripsammonts	15
Medell Flat	1520	tridentata	Typic Durargids	20

experiment was repeated with seeds collected in December 1983 and seedlings transplanted in May 1984. In each garden, 100 seedlings from each source were planted in a randomized block design. Seedling survival was recorded in October 1983 and April 1984. In April 1984, the height and maximum and minimum crown diameters of each plant were recorded. A biomass index was calculated from these data.

Precipitation was recorded at the garden. Because the gardens have been used for experiments for about 20 years, we had considerable precipitation data. Typical of weather in the Great Basin, the winter of 1982-83 was one of the wettest on record, and the winter of 1983-84 after January 1 was virtually without precipitation.

RESULTS AND DISCUSSION

Direct Seeding Experiment - December 1982

In March 1983, the first emergence was apparent from the fall seeding (fig. 1). Greatest initial emergence, 36 percent, occurred at the lowest and most arid site (Churchill Canyon #1). The two higher elevation mountain big sagebrush sites had no emergence (fig. 1). The relation between elevation and emergence continued through the early spring, except the number of seedlings at the lower elevation declined as emergence at higher elevations increased. Churchill Canyon #5 had very limited emergence throughout the spring.

The interplay in emergence among sites illustrates the basic role temperature and available moisture play in controlling germination in the Great Basin during spring germination periods. Because precipitation is largely out of phase with temperatures that permit growth, seeds in a sagebrush seedbed seem to be almost always too cold or too dry to germinate. The higher elevation sites have the greatest precipitation, but often are markedly colder than the more arid sites at lower elevation. Remember that the winter of 1982-83 ranks as one of the wettest in western Nevada's recorded history (table 2). Despite abundant precipitation at the Churchill Canyon #5 site during the spring of 1983, favorable temperatures and available moisture for germination in the seedbed never coincided (fig. 1).

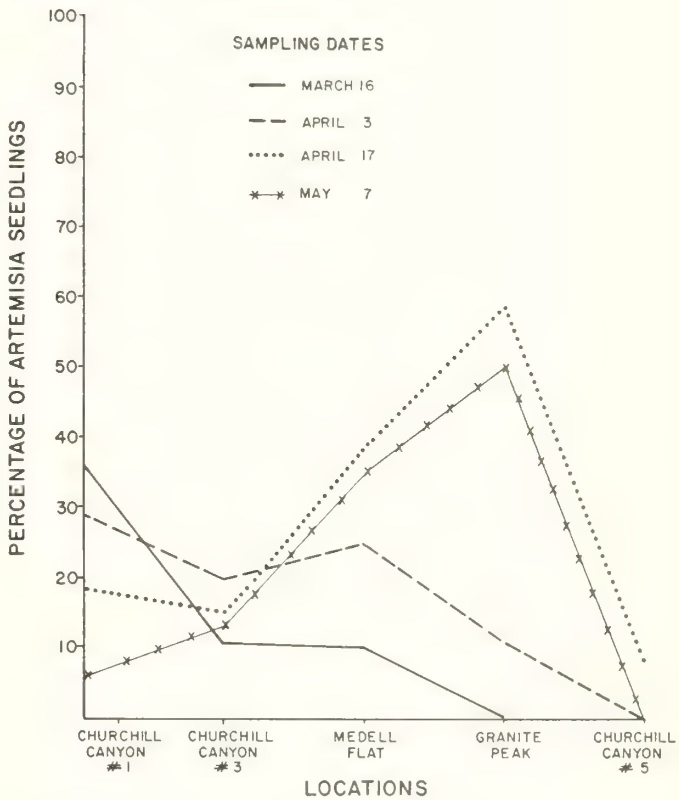

Figure 1.--Percent emergence of Artemisia tridentata seedlings in five reciprocal gardens at four sampling dates during the spring of 1983.

There was sufficient soil moisture at some sites during the spring and early summer of 1983 that the sagebrush seedlings persisted, even in relatively dense stands, in the artificial environments of the buried pots (table 3). The greatest seedling survival was at Granite Peak and Medell Flat. Seeds from Churchill Canyon #5 failed to germinate and establish at their site of collection, but had 82 percent seedling survival at the other mountain big sagebrush site. At the most arid site, Churchill Canyon #1, there were no differences among the sources in establishment by August 1, 1983.

Table 2.--Precipitation (cm) at the five seed collection and reciprocal garden locations in 1982-83 and 1983-84

Location	September-December		December-March		March-June		Total	
	1982-83	1983-84	1982-83	1983-84	1982-83	1983-84	1982-83	1983-84
	cm							
Granite Peak	13.2	11.7	21.3	8.4	10.2	2.3	44.7	22.4
Medell Flat	10.4	8.6	17.5	7.4	7.9	1.8	35.8	17.8
Churchill Canyon #1	7.6	4.8	10.7	5.1	5.3	1.0	23.6	10.9
Churchill Canyon #3	10.2	7.4	16.8	4.8	7.4	1.3	34.4	13.5
Churchill Canyon #5	13.0	12.7	20.6	5.8	9.9	1.5	43.5	20.0

Table 3.--Percentage establishment of big sagebrush seedlings in five reciprocal plantings. Seeds planted December 1982, data collected August 21, 1983[1]

Source	Garden location					Means of sources
	Granite Peak	Medell Flat	Churchill Canyon #1	Churchill Canyon #3	Churchill Canyon #5	
	percent					
Granite Peak	28bc	63a	0c	0c	0c	18y
Medell Flat	10bc	35b	5bc	3bc	0c	11z
Churchill Canyon #1	13bc	33bc	3bc	0c	2c	10z
Churchill Canyon #3	8bc	25bc	5bc	5bc	0c	10z
Churchill Canyon #5	82a	25bc	3bc	0c	0c	22y
Means of locations	28y	37y	3z	2z	0z	

[1]Means of sources at individual locations followed by the same letter (a through c) are not different at the 0.05 level of probability as determined by Duncan's multiple range test. Overall means (locations and sources compared separately) followed by the same letter (y or z) are not different at the 0.01 level of probability as determined by Duncan's multiple range test.

Direct Seeding Experiment - March 1983

Despite abundant precipitation in the spring of 1983, sagebrush seedling establishment was much lower from spring seeding than fall seeding (tables 3 and 4). There were no statistical differences (P=0.05) among the sources in establishment, but the two sources of mountain big sagebrush had the numerically highest establishment.

Direct Seeding Experiment - December 1983

There were three treatments in the direct seeding experiments established in the fall of 1983: (1) using the soils found on each site (duplication of the 1982 experiment), (2) using a constant soil at all sites, and (3) using a constant soil with marbles to provide favorable microtopography.

Using the soils native to the site for the direct seeding experiments produced big sagebrush seedlings only at the relatively low-elevation Medell Flat and Churchill Canyon #1 sites (table 5). Substituting a uniform soil at all locations produced similar results. The addition of marbles to the soil surface to provide more favorable microtopography increased seedling establishment at all locations except Churchill Canyon #5 (table 5). The two sources of mountain big sagebrush had higher establishment rates than the basin big sagebrush sources.

Table 4.--Percentage establishment of big sagebrush seedlings in five reciprocal plantings. Seeds planted March 1983, data collected August 1, 1983

Source	Garden location					Means of sources
	Granite Peak	Medell Flat	Churchill Canyon #1	Churchill Canyon #3	Churchill Canyon #5	
	percent					
Granite Peak	8	12	0	0	0	4
Medell Flat	2	2	2	0	0	1
Churchill Canyon #1	4	0	0	0	0	1
Churchill Canyon #3	2	2	0	0	0	1
Churchill Canyon #5	24	8	0	0	0	6
Means of locations	8	5	0	0	0	

able 5.--Percentage establishment of big sagebrush seedlings in five reciprocal plantings. Seeds planted March 1982, data collected April 30, 1984

Location	Treatment	Source of seeds: Granite Peak	Medell Flat	Churchill Canyon #1	Churchill Canyon #3	Churchill Canyon #5	Means of location
		percent					
Granite Peak	Location soil	0	0	0	0	0	0
	Constant soil	0	0	0	0	0	0
	Constant soil/marbles	18	2	4	6	10	8
Medell Flat	Location soil	4	0	0	0	16	4
	Constant soil	6	2	0	0	14	4
	Constant soil/marbles	36	8	6	10	32	18
Churchill Canyon #1	Location soil	6	0	0	0	4	2
	Constant soil	0	0	0	0	6	1
	Constant soil/marbles	18	4	6	0	24	10
Churchill Canyon #3	Location soil	0	0	0	0	0	0
	Constant soil	0	0	0	0	0	0
	Constant soil/marbles	6	0	0	0	3	2
Churchill Canyon #5	Location soil	0	0	0	0	0	0
	Constant soil	0	0	0	0	0	0
	Constant soil/marbles	0	0	0	0	0	0
Means of sources	Location soil	2	0	0	0	4	
	Constant soil	1	0	0	0	4	
	Constant soil/marbles	16	3	3	3	14	

The presence of microtopography, provided by the marbles, greatly enhanced the potential of the seedbed to support germination of the quite small big sagebrush seeds. This microtopography modified soil moisture, relative humidity, and temperature in the proximity of the big sagebrush seeds (Evans and Young 1972).

Direct Seeding Experiment - March 1984

Direct seeding in the spring of 1984 gave similar results to the 1983 fall seeding on the soils of the site (data not shown). Seedlings emerged only at Medell Flat and Churchill Canyon #1.

Transplant Experiments

The gardens have not been established long enough for survival to be a meaningful statistic. Initial establishment in the first growing season was over 95 percent in all gardens for all sources.

In April 1984, we sought to evaluate differences in the sizes of the plants from the various sources in the reciprocal gardens. To take into account differences in growth form (some plants are upright and others nearly decumbent) we calculated an index of above ground biomass as follows:

$$\text{biomass} = \text{height} \times \frac{\text{maximum} + \text{minimum diameter}}{2}$$

The largest plants for all gardens were the mountain big sagebrush plants from the Granite Peak and Churchill Canyon #5 sites (table 6). The basin big sagebrush plants were, after 1 year in the gardens, significantly (P=0.05) smaller.

Table 6.--Biomass (cubic meters) of Artemisia tridentata transplants in five reciprocal gardens. Biomass calculated by Biomass = $\frac{\text{height x maximum + minimum diameter}}{2}$. Data taken April, 1984 on plants transplanted to garden during May, 1983[1]

Source	Garden location: Granite Peak	Medell Flat	Churchill Canyon #1	Churchill Canyon #3	Churchill Canyon #5	Means of sources
Granite Peak	21b-d	26b	14e-g	13f-h	8hi	16a
Medell Flat	18c-f	15d-g	6i	6i	4i	10b
Churchill Canyon #1	24b	13f-h	4i	5i	6i	10b
Churchill Canyon #3	20b-e	22bc	5i	5i	5i	11b
Churchill Canyon #5	18c-f	39a	9g-i	13f-h	5i	17a
Means of locations	20b	23a	8cd	9c	5d	

[1]Means followed by the same letter are not significantly different at the 0.05 level of probability as determined by Duncan's multiple range test. Overall means for sources and locations compared separately.

The gardens supporting the largest plants were at Granite Peak and Medell Flat. Both of these sites have soils derived from decomposing granite compared to mixed alluvium from volcanic or mesovolcanic sources for the soils of the other sites. Plant size of the big sagebrush transplants was smallest at Churchill Canyon #5.

INTERPRETATION OF INITIAL RESULTS

This type of study obviously becomes more meaningful as the time base of observations increases. However, the initial results suggest some interactions of site potential and inherent potential of various collections of big sagebrush.

Seedling establishment of big sagebrush is obviously a rather high-risk venture, even in years of above average precipitation. In perspective, we should remember that, considering the longevity of big sagebrush plants, recruitment to the population is probably not required annually.

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FOLIAGE BIOMASS AND CRUDE TERPENOID PRODUCTIVITY OF BIG SAGEBRUSH

(ARTEMISIA TRIDENTATA)

Rick G. Kelsey

ABSTRACT: In spring, overwintering sagebrush leaves expanded in size diluting the concentration of chloroform extractable epidermal chemicals (crude terpenoids). Between June and December leaf biomass decreased one third, and crude terpenoid concentrations doubled. Fifty percent defoliation in late winter did not adversely affect growth, or crude terpenoid concentrations. Plants survived complete defoliation in late winter when leaf primordia and twigs were undamaged. A synthetic crude oil was made from the crude terpenoid extract. Sagebrush has the botanical and chemical characteristics of a desirable biocrude producing plant.

INTRODUCTION

Leaves of big sagebrush (Artemisia tridentata Nutt.) have been described as a two-component chemical system (Kelsey and others 1982). The epidermal surface represents the external component and is characterized by hydrocarbons and oxygenated hydrocarbons in the form of terpenoids stored in glandular trichomes (Kelsey and Shafizadeh 1980) and waxes that are part of the cuticle (Silva Fernandes and others 1964; Thomas 1976). These compounds are readily accessible and easily removed by washing fresh whole leaves in organic solvents. Drying and weighing the extract provides a quantitative measure of the epidermal chemicals, also called crude terpenoids (Kelsey and others 1982). Because of their high concentrations, and ease of removal, crude terpenoids might provide a renewable source of oxygenated hydrocarbons for energy, chemical feedstocks, or specialty chemicals. Compounds in glandular trichomes are also of interest because of their potential as chemical defenses against herbivores (Kelsey and others 1983), pathogens, and associated vegetation (Klarich and Weaver 1973; Weaver and Klarich 1977; Kelsey and others 1978).

Constituents within leaves represent the internal chemical component characterized by cell wall polymers, protein, nonstructural carbohydrates, and some lipids. Extraction of crude terpenoids with chloroform removed all of the monoterpenes, greatly reduced ether extractives (crude fat), had minimal effect on protein content, and concentrated nonstructural carbohydrates in the residue (Kelsey and others 1982). This suggests an improved nutritional quality and potential for use as a livestock feed. Removing crude terpenoids increased digestibility by an average of 15 percent in vitro, using rumen fluid from sheep (Striby and others 1982).

Yield of crude terpenoids from a plant depends on the quantity of foliage and concentration of epidermal chemicals. Peak foliage biomass occurs after spring growth, before overwintering leaves begin to drop, when crude terpenoids are at their lowest concentration. Conversely, in fall and winter, leaf biomass is minimal and crude terpenoid content is at its highest (Kelsey and others 1982). In which season would the greatest yield of epidermal chemicals from a plant occur?

In spring, sagebrush growth began when all overwintering leaves (not just those near the leaf primordia) expanded and became physiologically active, as indicated by increasing quantities of crude protein and total nonstructural carbohydrates (Kelsey and others 1982). Simultaneously, there was a decline in crude terpenoid concentration. Data suggested the epidermal chemicals were diluted by increased leaf size. If so, crude terpenoid concentration should remain relatively constant when measured in quantity per leaf rather than quantity per unit of dry matter. If chemicals remain on the epidermal surface during spring growth, the yield per plant should remain high, but extraction would require processing more tissue.

Portions of a sagebrush crown can be harvested without adversely affecting its growth. The response depends upon the amount of tissue removed and phenological stage, or season harvested (Cook and Stoddart 1960; Wright 1970; Cook 1971). Partial defoliation by herbivores (rabbits, sage grouse, antelope, and mule deer) can occur throughout the year, but is usually most frequent during late fall, winter, and early spring months when other sources of forage are unavailable (Sundstrom and others 1973; Wallestad 1975; Green and Flinders 1980; Welch and others 1981). Bryant (1981) reports that adventitious shoots sprouting from boreal trees after heavy browsing by snowshoe hares contain significantly higher concentrations (at least double) of ether-soluble resins compared to mature-growth-form twigs. Higher resin contents in the adventitious

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shoots make them unpalatable to hares, thus providing the trees with some protection against herbivory. Could chemical changes associated with herbivore defoliation of sagebrush influence palatability of the regrowth? If defoliation does cause changes in crude terpenoid concentrations, what are the implications for producing high energy compounds?

The objectives of this research were to provide answers for the following questions:

1. During what time of year would the yield of epidermal chemicals from whole sagebrush plants be greatest?
2. When overwintering sagebrush leaves expand during spring growth, is there a change in the quantity of epidermal chemicals on the leaf surface?
3. What effect does defoliation have on the growth and vigor of sagebrush plants, and what is the crude terpenoid concentration in the regrowth?
4. Could sagebrush be used as a renewable source of biocrude chemicals, or other commercial materials?
5. Do data from the above experiments provide new insight into the hypothesis that epidermal chemicals of sagebrush constitute a chemical defense mechanism against herbivores.

MATERIALS AND METHODS

Crude Terpenoid Analysis

In the field, plant samples collected for crude terpenoid analysis were placed in Ziploc plastic bags, transported on ice to the lab, sealed in a second Ziploc bag, and stored in the freezer. Fresh frozen tissue was considered fresh since freezing caused no external signs of tissue damage. Before analysis each sample was frozen with liquid nitrogen; leaves were dislodged and separated from the woody tissue and then resealed in a plastic bag until adjusted to room temperature. If leaves could not be analyzed immediately, they were returned to the freezer in double plastic bags. After reaching room temperature, duplicate samples were weighed for extraction (2-8 g) and moisture content determination (1-2 g, 100 °C overnight 15 hours, cooled in a desiccator 30 minutes, then weighed). Leaves were washed for five minutes with chloroform (24 ml per g of fresh tissue) then filtered through coarse paper (Schleicher and Schuell sharkskin, cut to 14-cm diameter) into a preweighed flask. Chloroform was removed on a roto-evaporator with reduced pressure and a water bath (30-40 °C). Final traces of chloroform were removed by increasing the water bath temperature to 60-65 °C for one hour. The flask was wiped dry, desiccated for 30 minutes, and weighed.

In previous experiments, all crude terpenoid measurements have been restricted to leaf tissue in order to make accurate comparisons quantitatively on a seasonal basis and between taxa. Inclusion of woody tissue has been avoided because the proportion in current year's growth varies considerably between taxa. This experiment was conducted to see how crude terpenoid concentrations in other tissues compare with those in the leaves. A large composite sample of basin big sagebrush (Artemisia tridentata Nutt. ssp. tridentata) was collected at Perma, MT, on August 31, 1981, sealed in a plastic bag, transported on ice, and stored at subfreezing temperatures. Four tissues (leaves, twigs, twigs with attached leaves, and flower heads) were analyzed in triplicate for crude terpenoids.

Study Site

The study site for all field experiments discussed below was located in a stand of mountain big sagebrush (A. tridentata ssp. vaseyana (Rydb.) Beetle) at Lavalle Creek near Missoula, MT. The area was grazed each summer by cattle, but this had minimal effect on the experimental plants.

Overwintering Leaf Measurements

Previous studies demonstrated that all overwintering leaves expanded in length and width during spring (Kelsey and others 1982). Accompanying increases in dry weight could dilute the crude terpenoids, causing a decreased concentration when expressed as a percentage of dry weight. Effects of dry matter changes were eliminated by measuring the quantity of crude terpenoids from 200 overwintering leaves before and after spring growth. On March 9, 1982, prior to any growth, eight mature shrubs were tagged and sampled. Two hundred leaves were analyzed for crude terpenoids (using the same ratio of solvent to tissue given above), 100 were ovendried (as above), and 10 were measured fresh for length and width. All leaves were randomly selected. The same plants were resampled June 8, 1982, after leaf expansion. Before freezing with liquid nitrogen, all new tissue was removed, and the remaining overwintering leaves were analyzed again as described.

Spring Changes in Twig Biomass

To measure changes in foliage biomass during spring growth, five mature plants were selected for study on April 2, 1982. Three pairs of twigs were marked on each plant. Each pair was carefully chosen to be approximately equal in length amount of woody tissue, and number of leaves. One twig of each pair was clipped, returned to the laboratory, and air-dried. Leaves and woody tissue were separated, then ovendried and weighed. The second twig of each pair was clipped June 8, 1982, and processed in the same manner.

Spring and Fall Foliage Biomass

Seasonal change in leaf biomass was determined on 10 pairs of mature plants. On June 17, 1982,

hrub pairs growing in close proximity were hosen for similarity in crown dimensions length, width, height) and leaf biomass (ocular stimate). One plant of each pair was clipped at round level, returned to the laboratory, and ir-dried. Leaves were separated from woody tems, ovendried, and weighed. The remaining lants were clipped December 2, 1982, and the rocedure repeated.

ffects of 50 Percent Defoliation

he following experiment was designed to deter- ine what effect removing 50 percent of the agebrush foliage in late winter would have on lant growth, biomass, and crude terpenoid con- entrations. On March 10, 1982, prior to the tart of spring growth, five pairs of shrubs were arked and measured (maximum live crown length, aximum live crown width perpendicular to length, nd height of tallest vegetative branch). Pairs ere growing close to one another and had similar rown sizes and leaf biomass. Between March 23 nd 26, 1982, the treatment plant of each pair as clipped to remove 50 percent (ocular esti- ate) of the leaf tissue on every twig throughout he crown. Clippings were carefully gathered, ealed in a plastic bag, transported to the lab n ice, and weighed fresh. Duplicate subsamples ere ovendried to calculate dry weights and per- entage of leaf tissue. The remaining fresh issue was frozen and analyzed for crude ter- enoids. A small sample of leaves was gathered rom the control plant at the same time the reatment shrub was clipped; it was frozen and nalyzed for crude terpenoids. One year later etween March 8 and 21, 1983, plants were clipped second time and analyzed as before. At the end f the second growing season, on November 22 and 9, 1983, live crown dimensions were remeasured or all plants. Foliage samples were clipped rom both treatment and control plants. After etermining fresh leaf weight, subsamples were emoved for duplicate moisture determinations and he remaining fresh leaves were analyzed for rude terpenoids. To measure total leaf biomass n the plants, each was clipped at ground level fter the foliage sample had been taken. Air- ried leaves were separated from woody tissue, vendried, and weighed. Dry weights of leaf amples collected for crude terpenoid analysis ere added to the leaf biomass for a total.

ffects of Complete Defoliation

n previous sagebrush clipping experiments, lants were defoliated by cutting twigs to remove ome portion of the current year's growth (Cook nd Stoddart 1960; Wright 1970; Cook 1971) in a anner similar to ungulate grazing. Carbohy- rates are stored in twigs at high concentrations uring the early portion of spring growth, but hen decline as new vegetative stems mature and lower stalks develop (Coyne and Cook 1970). To etermine how plants would respond if completely efoliated, without damaging leaf primordia or wigs, three pair of plants were selected as escribed in the previous experiment. Live crown dimensions were measured and all overwintering leaves carefully picked from the treatment plant (one pair set up on March 8, 26, and 30, 1982). The leaves were ovendried and weighed. One year later the defoliation was repeated (March 1, 2, 3, and 8, 1983); leaves were weighed fresh, ana- lyzed in duplicate for moisture content, and the remaining fresh tissue frozen for crude terpenoid analysis. A small leaf sample was also collected from each control plant for crude terpenoid ana- lysis. At the end of the 1983 growing season (November 22, 1983), live crown dimensions were remeasured, leaf samples were gathered for crude terpenoid analysis, and plants were clipped at ground level. Whole plants were air-dried; the leaves were removed, ovendried, and weighed. Leaf dry weights from samples used for crude ter- penoid measurements were determined as in the previous experiment and then added back for total leaf dry weight per plant.

Biocrude Production

Crude terpenoid extract is a mixture of monoter- penes, sesquiterpene lactones and cuticular waxes (Kelsey and others 1982) with a 21 percent oxygen content. Conversion of this material into a synthetic crude oil by hydrogenation was tested by Dr. Alan Peterson, Marathon Oil Company, Littleton, CO, using 200 g of extract, prepared as described above, but on a larger scale.

Screening for Biologically Active Compounds

Many terpenoids that occur in glandular trichomes on the epidermis of plants are biologically active, possessing antiherbivory, antifungal, antimicrobial, and herbicidal properties (Kelsey and others 1984). To test for active compounds with potential agricultural uses, crude terpenoid extracts were fractionated and sent to Dow Chemical Company, Walnut Creek, CA, for screening in a series of bioassays. Activities of interest included insecticidal, herbicidal, bactericidal, and fungicidal. In phase I of testing, crude terpenoid extracts were prepared from frozen foliage (stems and leaves combined) of eight sagebrush taxa: A. tridentata ssp. vaseyana-- high-elevation chemotype (Kelsey and others 1973; Bhadane and others 1975); A. tridentata ssp. vaseyana var. spiciformis (Osterh.) Beetle; A. tridentata ssp. tridentata; A. tridentata ssp. wyomingensis Beetle & Young; A. tripartita Rydb. ssp. tripartita; A. nova Nels.; A. cana Pursh ssp. viscidula (Osterh.) Beetle; and A. longiloba (Osterh.) Beetle collected between August 31 and September 4, 1981. A sample of A. tridentata ssp. vaseyana--low-elevation chemotype (Kelsey and others 1973) collected March 27, 1981, was also extracted.

Each extract was further fractionated into three components. Before removing all chloroform from the extract, it was transferred to a 3-neck round-bottom flask and dried on a roto-evaporator for one hour with vacuum and a 60-65 °C water bath. The residue was distilled with steam delivered to the extract by a glass tube inserted

through a rubber stopper in one of the three openings. Monoterpenes passed into a condenser and were collected over a column of water. The oil was drained into a vial, water drops removed with a pipette, and traces of water eliminated by leaving the open vial in a desiccator overnight. This was fraction 1. Water had condensed in the 3-neck flask during steam distillation and was evaporated on the roto-evaporator. The non-volatile residue left in the flask was dissolved in hot ethanol, transferred to a separatory funnel, and diluted with an equal volume of water. This solution was washed with several portions of hexane that were combined, evaporated, and dried (as for chloroform above) to give fraction 2. The ethanol-water was then extracted with chloroform which was evaporated and dried to give fraction 3. Leaves washed with chloroform for the crude terpenoid extract were air-dried and ground to pass a 20 mesh screen. This tissue was further extracted in methanol (10 ml per g) for 30 minutes with occasional stirring. The solution was filtered through sharkskin paper, evaporated, and dried (as above) to give fraction 4.

Since fraction 3 of all taxa, except A. tridentata ssp. vaseyana var. spiciformis, possessed some degree of fungicidal activity in phase I, this fraction was selected for futher study. Forty grams of fraction 3 were prepared for each of the following taxa: A. tridentata ssp. vaseyana; A. nova; A. tridentata ssp. tridentata; A. tripartita ssp. tripartita; and A. cana ssp. viscidula, collected between July 23 and September 17, 1982. Using column chromatography (7 x 68 cm column, packed wet with silica gel 60-200 mesh, and eluted with dichloromethane or chloroform with increasing amounts of ethyl acetate) these taxa samples were each divided into five parts and sent to Dow for further testing. Nine sesquiterpene lactones and two unknown flavonoids present in the extracts, but isolated previously, were also sent for testing.

Statistical Analysis

All data were analyzed statistically using the t-test for paired comparisons (Sokal and Rohlf 1981) at the 0.05 level of probability, unless otherwise stated.

RESULTS

Crude Terpenoid Content of Woody Twigs and Flower Heads

Leaves had the greatest concentration of crude terpenoids (table 1) and woody twigs the least; flower heads were intermediate. Samples containing leaves attached to twigs had the second highest concentration, just below leaves alone.

Spring Changes in Overwintering Leaves

Overwintering leaves increased in length and width on all eight plants examined (table 2).

Table 1.--Crude terpenoid concentrations in various tissues of basin big sagebrush (Artemisia tridentata ssp. tridentata)

Tissue	Crude terpenoids
	Percent dry weight
Leaves	[1]26.6 ± 1.0
Twigs with leaves	21.2 ± 1.0
Twigs	7.7 ± .6
Flower heads	14.4 ± .4

[1]± Standard deviation.

Table 2.--Changes in length, width, dry weight, and crude terpenoid concentrations for overwintering mountain big sagebrush leaves, during spring growth

	Amount of change[1]			
Plant	Length	Width	Dry weight	Crude terpenoid
	Millimeters per 10 leaves		Milligrams per 100 leaves	Milligram per 200 leaves
1	10.5	2.4	740.6	12.8
2	3.9	1.7	102.6	-16.1
3	11.8	2.2	725.7	31.4
4	4.0	1.3	-18.4	12.7
5	2.5	.0	103.8	-.9
6	2.6	.4	144.0	17.7
7	4.0	.7	206.1	-1.6
8	.7	.5	-49.4	-3.3
$\bar{X}$	[2]5.0	[2]1.2	[3]244.3	6.6

[1]Numbers represent amount of increase for the growth period between March 17 and June 8, 1982. - indicates decreases.
[2]Lengths and widths were significantly greater ($\alpha = 0.05$) in June.
[3]Dry weights were significantly greater ($\alpha = 0.10$) in June.

Table 3.--Paired twig biomass before (April) and after (June) spring growth of mountain big sagebrush, 1982

Plant	Biomass: Woody twig April	Woody twig June	Leaves April	Leaves June	Total April	Total June	Percent leaves in total April	Percent leaves in total June
	- - - - - - - - - - Milligrams dry weight - - - - - - - - - -							
1	[1]118	314	251	615	369	929	68.6	66.9
2	169	370	254	725	423	1,095	59.3	66.6
3	137	404	340	843	477	1,247	72.1	69.6
4	105	169	295	523	400	692	75.0	76.7
5	124	297	229	638	354	935	66.0	68.8
[2]$\bar{X}$	133	[3]321	272	[3]679	405	[3]1,000	67.7	[4]69.2

An average of three twigs per plant, except plant 4 with two twigs.
Averages calculated from 14 twig measurements on each date, instead of the five plant averages in the table.
Significantly greater than the April value (α = 0.001).
Not significantly different from the April value (α = 0.05).

This was accompanied by an increase in leaf weight for six of the eight plants. Overall, average dry weight of 100 leaves increased by 244.3 mg. These changes in leaf sizes were statistically significant. Crude terpenoid concentrations increased in four plants and decreased in four others. Three decreases, however, were quite small. The average concentration increased 6.6 mg per 200 leaves between March and June, but the difference was not significant. This supports the hypothesis that a spring decrease in crude terpenoid concentrations in old overwintering leaves, prior to new leaf growth, is primarily a dilution effect from increased dry matter. Consequently, the quantity of epidermal chemicals per leaf remains about the same, or maybe increases slightly.

Spring and Fall Foliage Biomass

Total twig biomass increased 2.5 times between April 2 and June 8 (table 3), with leaf (2.6 times) and woody twig (2.5 times) biomass changing in the same proportions. The ratio of leaf to woody tissue remained constant at about 2:1. Between June and December, leaf biomass decreased an average of 30.8 percent per plant (table 4). At the same time, average crude terpenoid concentration increased from 6.3 percent to 11.2 percent. Plants harvested in December would have provided 10 percent more crude terpenoid extract from about two-thirds the quantity of dry matter present in the spring.

Table 4.--Harvestable leaf biomass and crude terpenoid extract from mountain big sagebrush in spring and fall, 1982

Plant pair	Leaf biomass: June	December	December as percent of June	Estimated[1] crude terpenoid yields: June	December
	Grams dry weight			- - -Grams- - -	
1	39.2	35.2	89.9	2.5	3.9
2	96.2	58.6	60.9	6.1	6.6
3	43.1	22.6	52.4	2.7	2.5
4	119.3	72.9	61.1	7.5	8.2
5	178.5	79.8	44.7	11.2	8.9
6	61.9	36.0	58.2	3.9	4.0
7	34.8	41.9	120.3	2.2	4.7
8	56.7	47.6	84.1	3.6	5.3
9	125.1	69.4	55.5	7.9	7.8
10	62.1	40.4	65.0	3.9	4.5
TOTAL	[2]816.9	504.4	$\bar{X}$ = 69.2	51.5	56.4

[1]June yields were estimated using the June 8, 1982 average crude terpenoid concentration measured for 200 overwintering leaves, from each of eight plants ($\bar{X}$=6.3 percent). This compared with the 6.6 percent crude terpenoid concentration measured for all leaves in the crown on June 5, 1980 (see fig. 1, Kelsey and others 1982). November yields were calculated using the November 22 and 29, 1982, average crude terpenoid concentration ($\bar{X}$=11.2 percent) from seven control plants in the 50 percent and complete defoliation experiments.
[2]June values were significantly larger (α = 0.05).

Effects of 50 Percent Defoliation

Prior to clipping, treatment and control plants had similar crown sizes (table 5) and crude terpenoid concentrations (table 6) in the 50 percent defoliation experiment. After two growing seasons, control plants had significantly increased their crown sizes. Crowns of four defoliated plants were also larger, but still significantly smaller than controls. Nevertheless, treated plants continued to produce substantial foliage (table 7). At the end of the experiment, four out of five control plants had more foliage biomass than their corresponding treatment plants, but the difference was not significant. Each year after spring growth was complete, it was difficult to visually distinguish which shrubs had been clipped just a few months earlier. Defoliation had no effect on crude terpenoid concentrations (table 6).

Table 5.--Effect of 50 percent late winter defoliation, for two consecutive years, on crown size of mountain big sagebrush

Plant pair	Crown size[1]: Before clipping, March 1982[2]	Crown size[1]: Eight months after second clipping, November 1983[3]	Percent change
	- - - Centimeters - - -		
[4]1T	135	170	+26
1C	172	234	+36
2T	256	261	+2
2C	251	272	+8
3T	340	376	+11
3C	388	410	+6
4T	301	297	-1
4C	304	333	+10
5T	142	153	+8
5C	165	206	+25

[1]Crown length, width, and height measurements added together.
[2]When the experiment began, crown sizes of treatment and control plants were not significantly different.
[3]When the experiment ended, treatment crowns had not changed significantly from the start, but they were significantly smaller than control crowns. Control crowns did increase significantly in size during the experiment.
[4]T = treatment, 50 percent defoliated; C = control.

Table 6.--Effect of 50 percent late winter defoliation, for two consecutive years, on the crude terpenoid concentrations of mountain big sagebrush leaves

Plant pair	Crude terpenoid concentration: Before clipping, March 1982	One year after first clipping, March 1983	Eight months after second clipping, November 1983
	- - - Percent dry weight - - -		
[1]1T	7.5	10.5	10.1
1C	5.6	10.9	10.1
2T	9.8	16.2	13.0
2C	8.6	13.1	-
3T	7.8	10.9	11.4
3C	11.3	11.6	12.6
4T	9.6	14.1	13.0
4C	8.4	12.5	11.6
5T	7.1	11.3	11.2
5C	8.5	12.4	9.7
$\bar{X}$T	[2]8.4	[2]12.6	[2]11.4
$\bar{X}$C	8.5	12.1	11.0

[1]T = treatment, 50 percent defoliated; C = control.
[2]No significant difference between treatment and control.

Table 7.--Biomass from 50 percent late winter defoliated mountain big sagebrush, after two consecutive years of treatment

Plant pair	Twig and leaf biomass from 50 percent clip: First clipping, March 1982	Twig and leaf biomass from 50 percent clip: Second clipping, March 1983	Total leaf biomass: Eight months after second clipping, November 1983	Percent leaf in 50 percent clippings: March 1982	Percent leaf in 50 percent clippings: March 1983
	- - -Grams dry weight- - -				
[1]1T	14.6	30.5	[2]62.7	79.2	80.5
1C	-	-	91.1	-	-
2T	29.6	59.2	68.7	78.5	79.0
2C	-	-	97.7	-	-
3T	78.4	192.3	195.6	69.1	78.4
3C	-	-	367.2	-	-
4T	45.1	88.3	161.4	67.7	73.0
4C	-	-	151.8	-	-
5T	18.9	43.4	44.7	71.2	75.0
5C	-	-	57.5	-	-
$\bar{X}$				73.1	77.2

[1]T = treatment, 50 percent defoliated; C = control.
[2]No significant difference between treatment and control group.

Effects of Complete Defoliation

The response of completely defoliated plants appeared to be dependent on the amount of competition from associated shrubs. Plants in pair 1 were both growing with little competition from other sagebrush. The treated plant increased crown size and maintained leaf dry matter at 70 percent of the control (tables 8 and 9). Plant pair 2 grew closer to other shrubs and experienced more competition than pair 1. Live crown of the treated plant decreased 26 percent from its original size; leaf biomass was 53 percent of control. The third plant pair grew side by side, with completely overlapping root systems, but no competition from other shrubs. Weakening the competitive ability of the treated plant would directly benefit the control. Results indicate this type of relationship existed. Live crown size for the defoliated plant decreased 19 percent; leaf dry weight was only 7 percent of the control. Release from competition resulted in a 59 percent increase in the control crown size, the largest increase of any plant in either defoliation experiment. Live crown size of controls and treatments did not differ significantly at either the beginning or end of this experiment. Although foliage biomass was consistently greater on all control plants at the end of two years, this difference was not significant due in part to the small sample number. Leaf sizes were smaller on treated plants in both defoliation experiments, but the difference was most obvious when foliage had been completely removed. Crude terpenoid concentration was consistently higher in defoliated plants after the first year, but it was not significant (table 10). After a second treatment, crude terpenoid concentrations were equal in the two groups.

Table 8.--Effect of complete late winter defoliation, for two consecutive years, on crown size of mountain big sagebrush

Plant pair	Crown size[1]: Before defoliation, March 1982	Eight months after second defoliation, November 1983	Percent change 1982-83
	- - - -Centimeters- - - -		
[2]1T	[3]188	[4]204	8.5
1C	164	218	32.9
2T	149	110	-26.2
2C	149	156	4.7
3T	95	77	-18.9
3C	129	205	58.9

[1]Crown length, width, and height measurements combined.
[2]T = treatment, completely defoliated; C = control.
[3]No significant difference between treatment and control group.
[4]No significant difference between treatment and control group; controls March 1982 vs. controls November 1983; or treatments March 1982 vs. treatments November 1983.

Table 9.--Effect of complete late winter defoliation, for two consecutive years, on leaf biomass of mountain big sagebrush

Plant pair	Leaf biomass: First defoliation, March 1982	Second defoliation, March 1983	Eight months after second defoliation, November 1983
	- - - - - - Grams dry weight - - - - - -		
[1]1T	45.6	62.3	[2]63.4
1C	-	-	91.1
2T	12.8	14.5	12.9
2C	-	-	24.2
3T	10.0	13.2	8.1
3C	-	-	124.7

[1]T = treatment, completely defoliated; C = control.
[2]No significant difference between treatment and control group.

Table 10.--Effect of complete late winter defoliation, for two consecutive years, on crude terpenoid concentrations of mountain big sagebrush

Plant pair	Crude terpenoid concentration: One year after first defoliation, March 1983	Eight months after second defoliation, November 1983
	- - - - - Percent dry weight - - - - -	
[1]1T	[2]17.6	[2]13.7
1C	12.5	12.0
2T	16.5	9.9
2C	10.1	13.1
3T	14.4	14.7
3C	13.5	12.4
$\bar{X}$T	16.2	12.8
$\bar{X}$C	12.0	12.5

[1]T = treatment, completely defoliated; C = control.
[2]No significant difference between treatment and control group.

Biocrude Production

Plant products have the potential to be utilized as renewable sources of fuels and chemicals (Weisz and others 1979; Buchanan and others 1980; Calvin 1980; Johnson and Hinman 1980; Buchanan and Duke 1981; Wang and Huffman 1981). Monoterpenes and sesquiterpenes can be burned directly as liquid fuel (Calvin 1980; Wang and Huffman 1981) or catalytically cracked into gasoline (Weisz and others 1979; Calvin 1980). Experiments at Marathon Oil indicated that direct catalytic cracking of the crude terpenoid extract in a conventional fluid catalytic cracking unit was not an attractive method for producing liquid fuels, because of the relatively high oxygen (21 percent) content. A desired alternative was to produce a synthetic crude oil (biocrude) by hydrogenating the extract to remove oxygen. The resulting oily liquid contained 87.97 percent carbon, 11.94 percent hydrogen, 0.11 percent nitrogen, 0.07 percent sulfur, and no oxygen, and could be refined by conventional methods. There is reason to believe that crude terpenoids could be upgraded by hydrotreating more easily than processing either shale oil or residual oils.

Screening for Biologically Active Compounds

In phase I of the screening program for biological activity by Dow Chemical Company, 36 plant extracts (four from each of nine chemotypes) were tested. Extracts had no agriculturally significant herbicidal or insecticidal activity. Twenty-five extracts were antimicrobial at 500, 250, or 100 ug/ml, and most were inhibitory toward more than one bacterial species. Anaerobic microbes were more sensitive to the extracts than aerobic bacteria. Of all four fractions from a taxa, the hexane soluble compounds in fraction 2 were most antimicrobial, followed by 3, 4, and 1. *Artemisia nova* fractions inhibited the greatest number of bacterial species.

Extracts demonstrated a rather broad spectrum of fungicidal activity for six fungi species, but mainly against *Piricularia oryzae* (systemic rice blast) and *Plasmopara viticola* (grape downy mildew). Four fractions inhibited systemic rice blast and 15 were active toward grape downy mildew. Within a sagebrush taxa fraction 3 was most frequently active, followed by 2, 4, and 1.

In phase II, the five most active third fractions were prepared fresh, divided into five parts by column chromatography and each part bioassayed. In addition, pure crystalline sesquiterpene lactones, known to be present in the extracts, were tested. With the exception of *A. tridentata* ssp. *tridentata*, all five column parts from each sagebrush taxa were inhibitory to rice blast growth. Grape downy mildew was no longer available for testing, but based on results of phase I this fungi would also have been inhibited by these fractions. Surprisingly, none of the sesquiterpene lactones inhibited systemic rice blast fungi, suggesting the active constituent(s) was not a major terpenoid compound. Unfortunately, Dow was phasing out their fungicidal research and was unable to further evaluate this activity.

DISCUSSION

In recent years, the possibility of utilizing plant constituents as a renewable source of high energy compounds (biocrude), and organic chemicals has been given serious attention (Buchanan and others 1980; Johnson and Hinman 1980; Wang and Huffman 1981). Plants capable of growing in semiarid and arid regions of the Southwestern United States and Mexico (Campos-Lopez and Roman-Alemany 1980; Johnson and Hinman 1980; McLaughlin and Hoffmann 1982) have been considered good candidates for development because they grow in hot, dry, sunny areas where inadequate water supplies have traditionally limited agriculture. Botanical as well as chemical characteristics of these plants are important (Buchanan and others 1978). Furthermore, methods used in conventional agriculture may have to be modified in order to function within the constraints associated with arid environments. A common goal for many plant growers and breeders has been to maximize dry matter production, but according to McLaughlin and others (1983) this may be inappropriate for biocrude crops on arid lands.

Sagebrush is already prolifically abundant in semiarid regions of the western United States ranging from Mexico to Canada (McArthur and Plummer 1978; McArthur and others 1979). Its presence has been estimated on 1.1 million square kilometers at varying densities (Beetle 1960). Although the plants play an important role as winter forage for wildlife and in soil stabilization (McArthur and others 1979), there are many areas where populations are more than adequate, or not needed at all. These shrubs, having evolved in western North America (McArthur and Plummer 1978; McArthur and others 1981), are adapted and well suited to their semiarid environments. It's unlikely they could be easily eradicated and replaced by other biocrude-producing plants. There are many examples illustrating that sagebrush can reinvade sites where it has been destroyed (Bleak and Miller 1955; Johnson 1969; Harniss and Murray 1973). When big sagebrush is heavily clipped, growth will decrease substantially, and it can kill the plants (Cook and Stoddart 1960; Cook 1971); but, as indicated in this study and in others (Wright 1970; Cook 1971), the crown can be partially defoliated every year in fall or winter without detrimental effects on growth or concentration of epidermal chemicals. If shrub eradication was the primary objective for a site, whole plants could be harvested and extracted. Continuous biocrude production might be achievable by partial crown harvesting on a yearly basis. To minimize physiological damage to the plants, cutting could take place any time of the year

ccept spring and early summer (Cook 1971). Fall : winter harvesting would have the least impact ı plant growth (Wright 1970; Cook 1971), and :ude terpenoid concentrations would be at their ıximum. Silver sagebrush (A. cana) and threetip ıgebrush (A. tripartita) might be ideal for ıarly harvesting since they regrow from root ›routs (Beetle 1960; White and Currie 1983). ›timal harvest time for silver sagebrush would .ffer from big sagebrush because of its deci- ıous nature (Beetle 1960).

: first thought, the potential for using sage- :ush as a biocrude-producing plant might seem .mited; however, on close examination the possi- .lity appears feasible. This is especially true : one accepts the premise that traditional agri- ıltural concepts may have to be modified in :der to effectively utilize arid and semiarid ınds in this country (McLaughlin and others)83).

ır studies have demonstrated that sagebrush pro- ıces chemicals (a complex mixture of hydrocar- ›ns and oxygenated hydrocarbons) on its ›idermal surface that are easily removed by ›lvent extraction (Kelsey and others 1982). :ude terpenoids are obtainable without drying or :inding the plant tissue and once isolated they ın be converted to a crude oil. Chemical yields ›uld be increased by further extracting the ıaves with a more polar solvent, ethanol or ıthanol (McLaughlin and Hoffmann 1982; Adams and :Chesney 1983) and including the woody tissues ıat contain about 8 percent extractables Shafizadeh and Buckwa 1970). Accumulation of :ude terpenoids on the leaves is not affected by ıhanced growth from fertilization (Kelsey, this :oceedings), or stress caused by heavy defo- iation (this study). Increasing biomass produc- ivity would directly increase the plant yield of iocrude chemicals.

ıemical analysis suggests that extracted foliage lso could be used as a livestock feed provided ıat large quantities of woody tissue were not ıcluded (Kelsey and others 1982). Ethanol- ctracted sagebrush leaves combined with alfalfa ıre readily consumed by sheep, and the mixture :ovided adequate nutrient quality for a main- ınance diet (Striby and others 1983). In vitro .gestibility of sagebrush was significantly ıproved after extraction with chloroform (Striby ıd others 1982). If shrub damage was not an ıportant consideration, cutting near the end of ›ring would provide maximum foliage quantity and ıtrient quality for livestock feed after extrac- .on. Crude terpenoid yields would still be .gh, although greater volumes of plant material ›uld have to be processed.

.her botanical characteristics of sagebrush ›ntribute to its desirability as a biocrude ant. Seed production is prolific (Harvey)81). Being wind-pollinated, the flower stalks se above the canopy so that seed collection is ıst, easy, and inexpensive (Plummer and others)68). Germination in the lab and field varies ·om poor to excellent depending on a variety of ıctors (McDonough and Harniss 1974; Harniss and McDonough 1976; Sabo and others 1979; Stidham and others 1980; Kelsey, this proceedings). A newly germinated sagebrush seedling is not very hardy and is susceptible to damage or death by frost, drought, competition, pathogens, and herbivores. Seedling survival in the field can be very low (Harvey 1981). Even though few seedlings are observed in natural sagebrush stands (Johnson 1969; Harniss and Murray 1973; Hazlett and Hoffman 1975), reproductive success is adequate to populate 1.1 million square kilometers (Beetle 1960) and reinvade areas treated for shrub eradication (Bleak and Miller 1955; Johnson 1969; Harniss and Murray 1973). Problems with new seedling mortality can be reduced by transplanting older seedlings from nursery stock and native stands (Plummer and others 1970; Long, this proceedings), or possibly rooted stem cuttings (Everett and others 1978). Growth is dependent on taxa, geographic origin of the taxa, chromosome numbers, and environmental influences (Harniss and McDonough 1975; McArthur and Welch 1982; Kelsey, this proceedings). Big sagebrush, the most widespread and abundant species, will grow on a variety of soils (Passey and Hugie 1962; McArthur and others 1979). It is interesting to note that basin big sagebrush (ssp. tridentata) is the fastest growing big sagebrush subspecies (McArthur and Welch 1982) and also produces the greatest quantities of crude terpenoids (Kelsey and others 1982). Out of 77 shrub species evaluated, big sagebrush had the best suitability index for use in restoring big game ranges in Utah (Plummer and others 1968). Many of the highest rated botanical characteristics--establishment, persistence, natural spread, growth rate, herbage yield, and availability of current growth--are also indicators of a good biocrude species.

The function of sagebrush chemicals as a defense against herbivores has just begun to be studied. The problem is very complex because the shrubs produce a variety of compounds that might be involved (monoterpenes, sesquiterpene lactones, highly volatile nonterpenoids, and phenolics) and their activities may be influenced by synergistic effects (Kelsey and others 1983). There is also a range of potentially affected herbivores (insects, livestock, and wildlife). Their responses to the various groups of compounds may be different. For example, Narjisse (1981) found that sheep discriminate against sagebrush monoterpene odor, whereas goats discriminate against the taste. Welch and others (1983) reported no correlation between the monoterpene content of five sagebrush taxa and their differential preference by mule deer. Much more needs to be learned before chemical interactions between sagebrush and herbivores can be fully understood.

Nevertheless, various observations and current knowledge imply that sagebrush plants are protected by a chemical defense mechanism. Native herbivores (pygmy rabbits, sage grouse, mule deer, and antelope) that have coevolved with the shrubs are heavy users compared to introduced domestic species (horses, goats, sheep, and cattle) (Sundstrom and others 1973; Hansen and

Reid 1975; Wallestad 1975; Olsen and Hansen 1977; Johnson 1979; Green and Flinders 1980; Narjisse 1981; Hanley and Hanley 1982). Given free access to the three subspecies of big sagebrush, mule deer prefer to utilize ssp. vaseyana over ssp. tridentata (Welch and others 1981; Sheehy and Winward 1981) even though the latter is more digestible (Welch and Pederson 1981; Striby and others 1982) and maintains a higher crude protein content during winter (Welch and McArthur 1979). Monoterpenes do not appear to be associated with this selection preference (Welch and others 1983). We have found other chemical differences that might be influencing mule deer. Subspecies tridentata consistently produces larger quantities of crude terpenoids, and it has greater concentrations of highly volatile nonterpenoid compounds such as methacrolein (Scholl and others 1977; Kelsey and others 1982; Striby and others 1982; Personius and others, unpublished results). In selection tests, grasshoppers preferred sagebrush extracted with chloroform over fresh tissue from the same plant (Geiselman and Kelsey, unpublished observations).

Furthermore, terpenoid constituents in glandular trichomes are concentrated on the tissue surface where they can most effectively exert a variety of biological activities (Kelsey and others 1984). Sagebrush monoterpenes and sesquiterpene lactones are located in glandular trichomes (Kelsey and Shafizadeh 1980) and these compounds are known to be antimicrobial (Nagy and others 1964; Nagy and Tengerdy 1967, 1968; Oh and others 1968; Weaver and Klarich 1976; Picman and Towers 1983), phytotoxic (McCahon and others 1973; Klarich and Weaver 1973; Weaver and Klarich 1977), and allergenic (Mitchell and others 1970; Mitchell and Dupuis 1971; Mitchell and Epstein 1974). It is not known if the highly volatile methacrolein is a glandular constituent, but it is recognized as a volatile animal toxin and mucus tissue irritant (Lewis and Tatken 1980). These shrubs are certainly armed with an arsenal of defense compounds.

Effectiveness of a chemical defense is dependent on the type of active compounds present and their quantities. Concentrations and compositions of sagebrush epidermal chemicals are genetically controlled with distinct differences between taxa (Kelsey and others 1982, 1983; Kelsey, this proceedings; Personius and others, unpublished results). Crude terpenoid concentrations are also influenced by environmental factors affecting growth; quantities vary from year to year within the same plant, depending on growing conditions (Kelsey and others 1982, and this study). Degree of protection is then regulated by genetic and environmental control of biosynthesis. As demonstrated in this study, sagebrush lacks the ability to increase crude terpenoid concentrations in response to defoliation, as a means of providing additional protection for the plants. Consequently, palatability of browsed sagebrush should remain relatively constant from year to year. Indeed, sagebrush taxa grazed by mule deer do maintain their level of palatability between years, as documented by animal preference for the same plants (Welch and others 1981).

During spring growth, overwintering leaves expand and increase their size diluting epidermal chemicals per unit of dry matter. Because active chemicals are concentrated on the surface rather than distributed throughout the tissue, increased size may have minimal impact on the protective quality of these compounds. This would seem particularly true for volatile deterrents (methacrolein) detectable by the olfactory sense of herbivores. If this is the case, overwintering leaves could expand without jeopardizing their defense. Conversely, if spring growth does weaken the chemical defense, it happens when plants may require less protection. Decreased apparency (Feeny 1976) results from the production of new foliage on associated vegetation that can be utilized by the herbivores (Willms and McLean 1978). Also, it may be unnecessary to have older leaves fully protected because shortly after leaf expansion stops they begin to senesce and drop from the plant. Although overwintering leaves are important for early spring metabolic activity, the plants can survive without them, particularly if the primordia remain undamaged.

Short internodes between sagebrush leaves cause rosette-like clusters near the stem tip (Diettert 1938). Older leaves surrounding the primordia could provide chemical protection until glandular trichomes have formed on newly developing leaves. Early appearance of glands (Diettert 1938) on the leaves is also suggestive of their protective role.

SUMMARY

1. Sagebrush crude terpenoid concentrations were highest in leaves (26.6 percent dry weight) followed by twigs with leaves (21.2 percent), flower heads (14.4 percent), and twigs (7.7 percent).
2. During spring, overwintering sagebrush leaves increased in length, width, and dry weight causing a dilution in the concentration of crude terpenoids. The quantity of epidermal chemicals remained about the same on each overwintering leaf as it expanded.
3. Twig biomass increased 2.5 times during spring growth, maintaining a 2:1 ratio of leaf to woody tissue.
4. Total plant leaf biomass in December was 30.8 percent lower than in June. Average leaf crude terpenoid concentrations were 11.2 percent and 6.3 percent, respectively. Whole plants harvested in December would provide quantities of crude terpenoid extract equal to, or greater than, whole plants harvested in June at peak foliage biomass.

5. Fifty percent defoliation of sagebrush plants in late winter for two consecutive years did not adversely affect growth and vigor. Crude terpenoid concentrations of defoliated plants did not differ from paired untreated controls.
6. Plants completely defoliated for two consecutive years, without damaging twigs or leaf primordia, continued to produce foliage. Growth and vigor seemed to depend on competition from other shrubs. Crude terpenoid concentrations of the regrowth remained similar to those of the untreated controls.
7. Hydrogenating the crude terpenoid extract to remove oxygen produced a high-quality crude oil (biocrude) that could be refined by conventional methods to liquid fuels and other organic chemicals.
8. Crude terpenoid extracts contained compounds that were antimicrobial, particularly toward anaerobic bacteria. Growth of several fungi was inhibited by extracts; two of the most sensitive fungi were causal organisms of systemic rice blast and grape downy mildew.
9. Based on botanical and chemical characteristics, sagebrush has potential to be used as a biocrude-producing plant in semiarid environments where it is adapted and occurs naturally.
10. Epidermal chemicals of sagebrush appear to function as a defense against herbivores.

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CHRYSOTHAMNUS NAUSEOSUS: A POTENTIAL SOURCE OF NATURAL RUBBER

W. K. Ostler, C. M. McKell, and S. White

ABSTRACT: Five taxa of rabbitbrush (Chrysothamnus nauseosus [Passas] Britt.) were evaluated for their potential for rubber production in a nine State area in the Western United States. Slope, aspect, elevation, geologic substrate, soil texture, pH, EC, soil phosphorus and potassium, plant height and diameter, plant weight, and plant water stress were all measured. Results indicate that rubber concentration is higher under stress conditions. Differences in rubber and resin contents were also identified among the five taxa. Chrysothamnus nauseosus ssp. consimilis var. viridulus had significantly greater percentages of rubber and resin content than the other four taxa. Age was shown to be positively correlated with rubber percentage.

INTRODUCTION

The genus Chrysothamnus (rabbitbrush) of Western North America belongs to the largest and most advanced of the flowering plant families, Compositae (Asteraceae, the sunflower family). The occurrence of rubber in C. nauseosus (rubber rabbitbrush) has long been known. The Western American Indians used rabbitbrush latex for chewing gum. In 1904, the presence of rubber in C. nauseosus was brought to the attention of the botanical world by A. J. Davidson, who sent a specimen to the University of California for identification and noted the Indians' use of it as gum (Hall and Goodspeed 1919). Fifteen years later, it was brought to national attention with the publication of Hall and Goodspeed's paper (1919) on Chrysothamnus rubber. They concluded that over 150,000 tons of rubber were available in native stands of Chrysothamnus in the Western United States, but very little research toward commercialization was done.

Initial work on rabbitbrush rubber quality was reported in a study by Dr. David Spence, Chairman of the Subcommittee on Rubber and Allied Substances of the National Research Council (Hall and Goodspeed 1919). He reported that the rubber was of good quality, vulcanized readily, and merited further investigation.

Paper presented at the Symposium: Biology of Artemisia and Chrysothamnus, Provo, UT, July 9-13, 1984.

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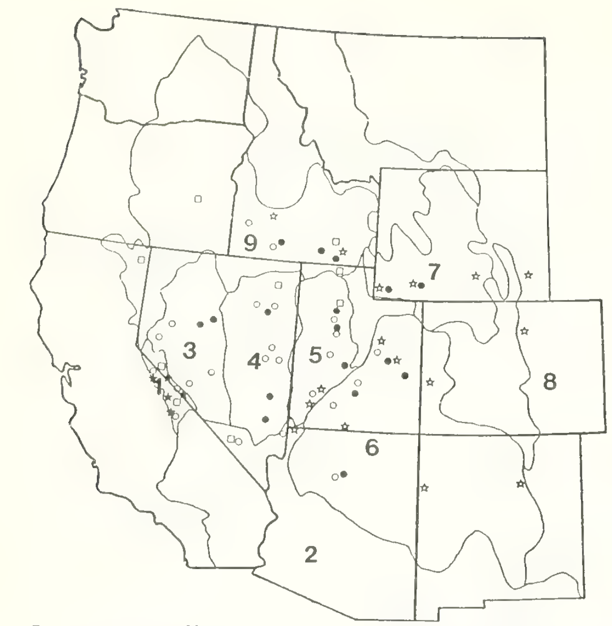
During World War II, the U.S. Department of Agriculture became interested in a domestic source of natural rubber due to potential blockages of foreign imports (Trumbull 1942; Doten 1942). Guayule (Parthenium argentatum) was eventually selected over rabbitbrush and other species for planting during the Emergency Rubber Project of the 1940's, principally because a guayule rubber production plant was operating in California and rubber had been commercially produced in Mexico and California.

The USDA recently evaluated over 100 plants having potential as hydrocarbon crops and rated rabbitbrush as having a very high potential for development (Buchanan and others 1978a, 1978b).

With this as a basis, NPI was able to obtain funding from National Science Foundation Small Business Innovation Research to evaluate rabbitbrush as a commercially viable rubber-producing species. The objectives of this study were to: (1) identify those subspecies of Chrysothamnus nauseosus that have a high rubber content, (2) identify environmental factors that may influence rubber accumulation, (3) determine growth rates and potential yields on agricultural and natural systems, and (4) initiate preliminary tests on rubber quality.

STUDY AREA AND TAXA OF INTEREST

The study area encompassed a major portion of the range of C. nauseosus in nine western states. A map of the area and study sites by subspecies is shown in figure 1. The area was divided into nine regions, based on floristic and physiographic features (Cronquist and others 1972) and included those recognized by Hall and Goodspeed (1919) in their work on rabbitbrush. Five high-yielding subspecies of C. nauseosus, previously identified by Hall and Goodspeed (1919) were the taxa of interest for this study. These include: C. n. ssp. consimilis; ssp. consimilis, var. viridulus; C. n. ssp. hololeucus, C. n. ssp. albicaulis, and C. n. ssp. graveolens. Chrysothamnus n. ssp. c. var. viridulus was recognized as a subspecies by Hall and Goodspeed in 1919, but is currently placed as a variety of C. n. ssp. consimilis (Anderson 1966). Due to its uniqueness from C. n. ssp. consimilis, in this analysis, it was kept as a unique taxa.



□C. n. ssp. albicaulis, ○ssp. hololeucus; ☆ssp. graveolens, ●C. n. c. var. consimilis; ★var. viridulus.

Figure 1.--The nine regions within the 10 states where field studies and rabbitbrush sampling sites occurred.

METHODS

Field Analysis

Within each region, three sample sites were selected for each of the subspecies found within that region. At each site, data were taken to identify the physical and biotic characteristics of the rubber rabbitbrush stand. Parameters measured included: slope, aspect, location, elevation, and geological substrate. In addition, a soil sample was taken at each site for analysis. Soils were analyzed for texture, pH, EC, phosphorus, and potassium (USDA 1969).

Six plants at each site were selected randomly for sampling using a criterion of size distribution. Height and two diameter measurements were recorded for each of these plants. Water stress readings (atm) were also taken using a Campbell J-14 plant pressure gauge.

To obtain a biomass volume value of the stand and determine growth rates, all six plants were cut at the soil line and weighed with a portable scale. The section at the base of each cut shrub was returned to the laboratory to determine age. A branch representative of the entire plant was removed from the plant and returned to the laboratory for chemical analysis to determine rubber content. A flowering sample was also collected and pressed at each site for taxonomic verification.

Chemical Analysis

Upon arrival at the laboratory, plants were oven dried at 140° F (60° C) for 48 to 72 hours and then defoliated. Each dried defoliated plant wa then processed through a Wiley mill using a 20-mesh screen and placed in a glass jar prior t extraction.

The extraction procedure was as follows: the contents of each jar, containing the milled residue of six plants, was shaken to thoroughly mix the material. A 30 to 40 g sample was removed and the oil extracted with acetone in a 500 ml Soxhlet apparatus for a minimum of 24 hr at 0.5 cycles/minute. This yielded a mixture of low molecular weight oil and high molecular weight resin. Each high molecular weight sample was further extracted for 24 hr with hexane to remove the natural rubber compounds.

The resultant hydrocarbon fraction from several different extractions was subsequently analyzed by nuclear magnetic resonance (NMR). This was used to determine the microstructure of chrysil rubber in order to compare it with published data for hevea rubber.

Data Analysis

The data were analyzed on a Univac 1176 using the statistical package, SPSS, developed at the University of Chicago and available nationwide (Nie and others 1975).

RESULTS AND DISCUSSION

Environmental Analysis

A total of 66 sites were sampled. Overall averages for the parameters sampled are given in table 1. The average rubber yield for all five subspecies combined was 1.3 percent. Total hydrocarbon content averaged 21 percent (rubber, oil, resin). Average height of all shrubs sampled was 29.1 inches (0.7 m), the average weight was 3.8 lb (1.7 kg), and the average age was 5 years. Plants grew in a wide variety of soils, however, the soils were generally sandy with fairly high pH's (7.9) and high EC's (4.1). Rubber yields were low, as woul be expected when averaging many populations. There was a wide divergence among individual plants and subspecies; individual yields ran as high as 6.57 percent.

A stepwise multiple regression was performed to determine if environmental factors, including plant size and age, influenced rubber content. The top five factors entering the stepwise regression were slope, elevation, stress, silt, and electrical conductivity (table 2). The results were significant at the 0.01 level, but only 28 percent of the variation was accounted for even with all five variables included in the regression equation. Again this is not unexpected since several taxa were involved in

Table 1.--Mean and standard deviations for environmental factors taken on the 66 rubber rabbitbrush sites over the entire study area

Environmental Factor	Mean	Standard deviation
Crown diameter (in)	40.2	5.7
Crown diameter (in)	34.4	4.8
Height (in)	29.1	5.4
Weight (lbs)	3.8	2.6
Age (yr)	5.1	1.6
Water stress (atm)	17.4	4.6
pH	7.9	.6
Sand (%)	59.3	20.7
Silt (%)	29.1	15.3
Clay (%)	11.9	6.1
Phosphorus (ppm)	11.4	12.9
EC (mmhos/cm)	4.1	3.1
Potassium (ppm)	207.1	116.1
Elevation (ft)	5305.3	1462.6
Slope (degrees)	4.1	4.4
Rubber (%)	1.3	.7
Oil (%)	5.7	2.6
Resin (%)	14.0	4.0

Table 2.--The top five factors that entered the multiple regression to determine what factors were associated with rubber concentrations (n=66)

Independent variables	Cumulative R	Sign	Significance
Slope	0.315	-	0.05
Elevation	0.412	-	0.01
Stress	0.459	+	0.01
Silt	0.502	-	0.01
Soil EC	0.531	+	0.01

the analysis. The parameters selected by the multiple regression indicate that rubber concentration is higher under stress conditions. Another rubber-producing species, guayule, has been noted to produce similar response (Campos-Lopez and McGinnis 1978; Ostler and others 1983).

It has been shown that rubber content is greater in older tissues, particularly near the soil line (Hall and Goodspeed 1919). A regression was run to determine average increase in rubber content in successively older tissues (fig. 2). The regression shows a significant linear relationship between age of the tissue and rubber content. This relationship is important when considering the economics of growing rabbitbrush commercially because not only will weight of the plants increase over time, but the rubber content of the plants will also increase, giving a multiplication effect.

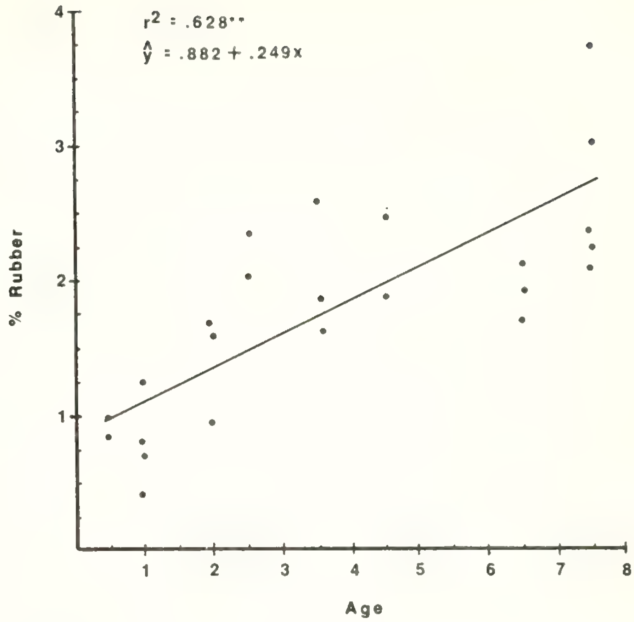


Figure 2.--Regression of rubber content and age (data extracted from Hall and Goodspeed 1919).

Analysis of Subspecies

To assess the influence that the genetic makeup of the plant may exert on rubber production, an analysis of variance was performed using subspecies as an independent variable to test its effect on the other parameters sampled. Only three parameters were significantly different among the subspecies. The one that is particularly interesting is rubber content (fig. 3). *Chrysothamnus nauseosus* ssp. *consimilis* var. *viridulus* is significantly higher than any of the other subspecies including *C. n.* ssp. *c.* var. *consimilis*. Indeed, var. *viridulus* average values for rubber content more than doubled *C. n.* ssp. *hololeucus*, the closest subspecies. This suggests that rubber content has strong genetic controls. Efforts to increase rubber production should be directed at selecting high rubber-producing strains.

A multiple regression performed on *C. n.* ssp. *c.* var. *viridulus* showed that plant size, measured as crown diameter, also is associated positively with rubber content. The "r" value was 0.893, which is significant at the 0.05 level. (Note: there were only three degrees of freedom).

Separate multiple regressions were run for each of the remaining subspecies using rubber content as the independent variable. The rankings of the dependent variable differed for each subspecies, but the same factors identified in the multiple regression using all sites were the major factors common to most subspecies, i.e., stress +, elevation -, EC +.

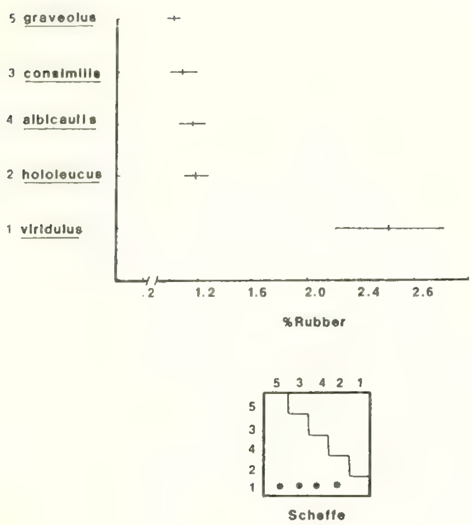


Figure 3.--The results of the analysis of variance for the percentage rubber content in rabbitbrush. The means and standard errors are located in the upper graph. Below are pairwise comparisons using the Scheffe procedure.

Growth Rates

To determine growth rates and yield in the field, the average weight (table 1) was divided by the average age. This yielded a value of .75 lb/yr (340 g/yr). This assumes that the growth is linear, which is certainly not true for the entire life of the plant, but may be appropriate for the first several years.

Growth rates from plants that had been clipped or hedged and allowed to grow for 2 years yielded average values of 1.1 lb/yr (510 g/yr) (McKell and Van Epps 1980; McKell and others 1981). These values are probably very comparable to what would be expected from an agricultural setting of Chrysothamnus in which harvest would take only the above-ground growth and leave the root system intact for regrowth.

Using the conservative growth rate of 1.1 lb/yr (500 g/yr), one can then calculate potential yields from agricultural systems. If one assumes 3 ft (91 cm) centers for the planting, this would require 4,842 plants/acre (11 964 plants/ha). At this spacing, in 5 years the canopy would be completely closed given average crown dimension obtained from this report. In 5 years, these plants would yield 533 lb of rubber per acre (598.2 kg/ha).

These figures are very conservative. Only two percent rubber content is assumed and growth rates are predicted to be the same as in native stands, which have generally high competition rates. If the plants contained a rubber content equivalent to the best native stock found, the yield would increase to 1,600 lb of rubber per acre (1 794 kg/ha) over 5 years. At 1983 prices of $0.46/lb (Wall Street Journal, Feb. 8, 1983) this would yield $736.00/acre or $1,812/ha worth of rubber. With competition control, these figures may increase conservatively at least another 50 percent, enabling reduction in the growing time to 3 years.

Rubber Quality

NMR analysis was performed on fresh extracted samples of C. n. ssp. albicaulis to determine the type of bonding of the carbon chain. Chrysothamnus n. ssp. albicaulis was selected because it grows very near NPI's research facility. Extracting and processing could be done quickly to avoid any decomposition of the rubber molecules. The results of the NMR as well as a comparison with hevea are shown in figure 4. The peaks are nearly identical and confirm that the rubber is composed of cis-isoprene molecules.

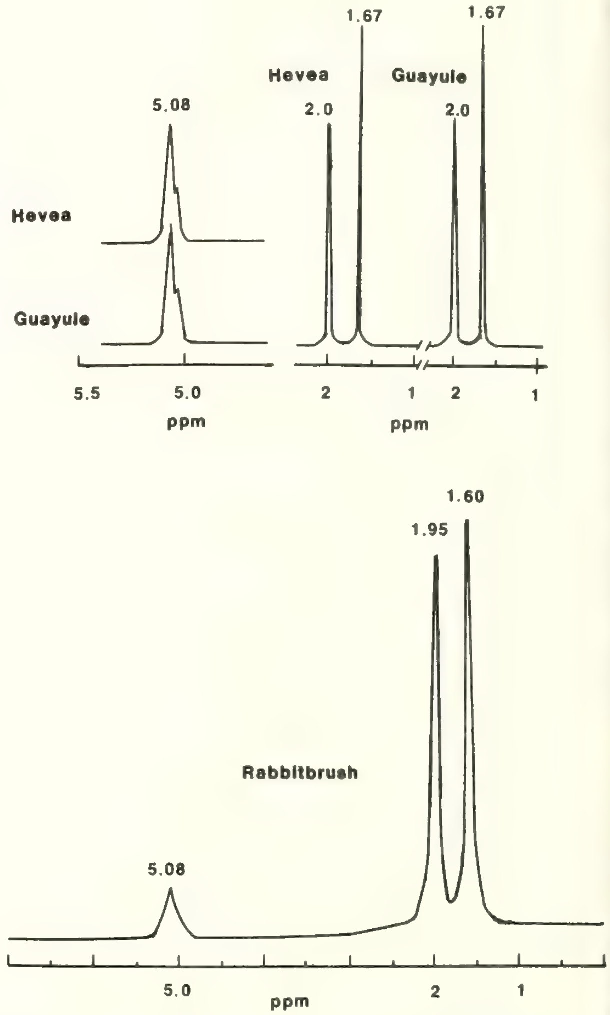


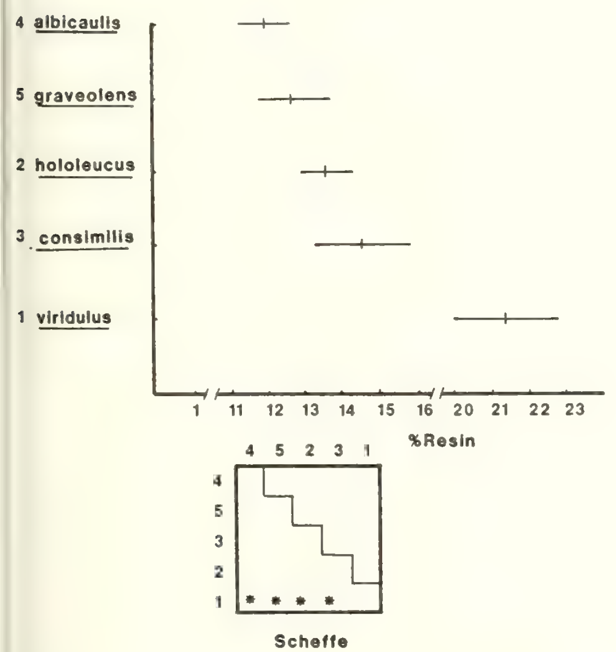
Figure 4.--Results of Nuclear Magnetic Resonance (NMR) of hevea, guayule, and rubber rabbitbrush. Rabbitbrush is on a larger scale.

reliminary tests on rubber quality have all been ncouraging, confirming the hypothesis that hrysil rubber is a good quality rubber. Second evel studies on quality need to be undertaken to etermine its acceptance and usefulness in the arket place.

nalysis of Resins and Oil

nother aspect that would enhance the economic easibility of growing Chrysothamnus nauseosus ommercially is the discovery of a high percentage f resins and oils in rabbitbrush tissue (table). Preliminary results showed that resins veraged 14 percent and oil six percent. The esin may prove to be a more valuable resource han the rubber. The samples for resin and oil ere from 1- to 2-year-old growth. Their values re higher than those determined by whole plant nalysis, but these would be the portions most asily harvested in a plantation-type operation.

o test if subspecies varied in their resin ontent, an analysis of variance was performed. he results were very similar to those reported or rubber content. Only C. n. ssp. c. var. iridulus was significantly different from the ther subspecies (fig. 5). This further trengthens the value of C. n. ssp. c. var iridulus as the subspecies with which to start elective breeding and improvement for ommercial production.



'igure 5.--The results of the analysis of variance or the resin content. The means and standard rrors are located in the upper graph. Below are airwise comparisons using the Scheffe procedure.

CONCLUSIONS

This study was beneficial in several areas which needed to be confirmed and verified before further work could be undertaken on the development of this potential source of domestic rubber. Perhaps the most important is the domination of genetic influence on Chrysothamnus nauseosus rubber production as illustrated by the analysis of variance. Having a strong degree of genetic constancy is important to breeding programs and subsequent trial plots.

Subspecies of C. nauseosus are also capable of interbreeding (McArthur and others 1978, 1979; McArthur 1984). This would facilitate the transfer and selection of genes for higher rubber content to other subspecies. Genetic amplitude is extremely great in these subspecies of rabbitbrush. They occur throughout western North America from hot desert valleys of California and Arizona to cold valleys and foothill slopes of southern Canada. The species characteristically occupies marginal land and invades into abused or overgrazed areas. It is very salt tolerant and actually shows slightly higher rubber content when in a stressful environment.

Average rubber values are low, but one must recognize that no genetic selections have been made on rabbitbrush. Indeed, less than 500 plants have ever been tested for rubber content. If individual specimen contents discovered thus far run as high as 6.57 percent (Hall and Goodspeed 1919), it appears feasible that this figure could be doubled by genetic selection, as has been done with guayule (McGinnes and Haase 1975; Campos-Lopez and McGinnes 1978). The growth rates of rabbitbrush are very high in comparison to guayule.

Rabbitbrush is widely distributed throughout western North America where winter temperatures are often below -20° F (-30° C). Thus, its potential range for cultivation and growth far exceeds that of any other rubber-producing plant in the area. In addition, it grows on marginal land and alkaline soils currently unused or unusable for agricultural crops. Rabbitbrush is also very resistant to mowing or harvesting. It rapidly resprouts from a cut stump, making it ideal for a continuous cropping system with several harvests through the life of the plant. The potential for rubber production from rabbitbrush appears very promising. Research should be directed toward genetic selection and improvement.

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CONTAINER NURSERY PRODUCTION OF ARTEMISIA AND CHRYSOTHAMNUS SPECIES

Lynn E. Long

BSTRACT: Several thousand sagebrush and abbitbrush seedlings are grown each year at lants of the Wild Nursery in eastern Washington. eed is stratified and sown directly into Ray each Supercells. Temperatures, soil moisture, nd nutrients are carefully monitored throughout he growing season. By mid-August plants are of ufficient size to undergo a hardening process. lants can be shipped in early fall or spring.

NTRODUCTION

lants of the Wild is a native plant nursery ocated approximately 50 miles south of Coeur 'Alene, ID and Spokane, WA in Tekoa, Whitman ounty, WA. Since 1980 we have grown native lants for reclamation and revegetation projects hroughout the West. Our current production is ver 250,000 plants per year. We maintain a rowing inventory of 1, 2, and 5 gallon plants. e are in an ideal location for growing a wide ange of native plants. Located in the ntermountain region of the Northwest, we are djacent to the dry desert regions of eastern ashington, eastern Oregon, and southern Idaho and et within a very short distance of the forests of estern Washington, western Oregon, and northern daho. It is largely for this reason that our lant list is so diverse. We grow 75 species of lants ranging from red alder and mountain uckleberry to fourwing saltbush and antelope itterbrush. Included in this list are Artemisia ana, A. frigida, A. tridentata ssp. tridentata, . tridentata ssp. wyomingensis, A. tridentata sp. vaseyana, and two species of rabbitbrush, hrysothamnus nauseosus and C. viscidiflorus.

HE CONTAINERS

ır standard tube is the 10 inch^3 Ray Leach upercell. This tube has several advantages over ther types of containers, including the ease with hich plants can be consolidated both after ermination and before hardening and shipping. ince each tube is a separate unit, tubes in which ermination did not take place can be removed. oreover, before moving to the shadehouse for hardening and eventual shipping, undersized plants can be removed and allowed to grow for a longer period in the greenhouse. This allows more effective utilization of our greenhouse space and shipment of only the strongest plants.

GROWING MEDIUM

Growing medium is composed of 50 percent sphagnum peat and 50 percent number 2 horticulture grade vermiculite. Dolomite lime is added to the medium at the rate of 5 pounds (11 kg) per cubic yard, along with 5 pounds (11 kg) of calcium carbonate lime. This raises the pH to neutral or slightly alkaline when growing sagebrush, rabbitbrush, or other species that prefer an alkaline soil. The coarse vermiculite allows for better root aeration and drying, which is important in growing many desert species.

SEED SOURCES

Seed is obtained from commercial sources throughout the Western United States. Since many of our plants are grown on a speculation basis, it is impossible to exactly match seed sources with planting sites for these plants. However, whenever possible we grow plants on a contract basis and occasionally customers will collect site-specific seed. This, of course, requires planning and enough lead time to collect the seed and grow the plants.

SEED GERMINATION

Due to erratic germination of sagebrush and rabbitbrush seed, we normally try to obtain several seedlots of each species. This will ensure that one or more seedlots will contain viable, nondormant seed. A germination test is performed on each seedlot before it is sown. A few seeds are placed on a moistened blotter in a tray and subsequently placed in a germinator set at 68° F (20° C). Germination should be complete within 10 to 14 days. The results determine whether to sow a particular lot, and, if so, how much seed to place in each tube. In the past, germination of sagebrush and rabbitbrush seed has been erratic and unpredictable. Seed that is over 1 year old is more likely to be dormant, or dead, than fresh seed. Frequently, however, seed that is less than 1 year old will show high viability as indicated by a tetrazolium test, but will fail

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aper presented at the Symposium: Biology of rtemisia and Chrysothamnus, Provo, UT, July 9-13, 984.

ynn E. Long is nursery manager and plant athologist at Plants of the Wild Nursery (Palouse eed Co.), Tekoa, WA.

to germinate. These lots are obviously dormant. Attempts were made to break this dormancy by stratifying the seed at 41° F (5° C) for up to 6 months and by subjecting stratified seed to freezing and thawing. Neither technique appreciably increased germination levels. It is for this reason that several different seedlots of fresh seed are tested before sowing.

When seed is received from the supplier it is held in a viable, nondormant state until planting by placing the seed in polyethylene bags three layers thick. Bags are then sealed and stored at 37° F (3° C). It is possible to keep seed in this state for several months. At the same time that germination testing is done, the remaining seed is soaked overnight in water and then placed in a porous cloth bag. This bag is then placed in a tray and covered with vermiculite. The seed is stratified at 41° F (5° C) for up to 15 days. This stratification provides a more rapid and uniform germination.

The seed is sown directly into the Supercell tube, normally in April or May. The quantity of seed sown depends on the outcome of the germination test. Enough seed is placed into each tube to assure that at least one germinant will be present. Approximately 1 month after seeding the plants are thinned, leaving only the strongest plant in each tube. Stratified seed is sown by hand due to the moistened condition. Once the seed is sown, a thin (ca. 1 mm) layer of Perlite is sprinkled over the seed. This covering acts as a mulch and holds moisture at the seed level. The seed is lightly sprinkled with water at least three times per day to replenish moisture. Germination should begin within 2 or 3 days. Sprinkling continues until germination is nearly complete, usually within 10 to 14 days.

WATERING AND FERTILIZING

Once germination is complete, fertilization begins. We use commercial fertilizers that contain all the major and minor elements needed. To begin, we use a 9-45-15 formulation at the rate of 100 ppm nitrogen followed in 3 weeks with 20-10-20 at the rate of 200 ppm nitrogen. The seedlings are fertilized each time they are watered, normally with 20-10-20; but if growth is too rapid 9-45-15 is used for one or two waterings. Our main concern is to develop a good caliper and root system with a proportional shoot. Therefore, watering and fertilization are most critical. To avoid root rot and to prevent the plants from becoming spindly, they are not watered until the soil is nearly dry. At that time we water to saturation.

GROWING TEMPERATURES

The growing temperature for sagebrush is approximately 80° F (27° C), but average greenhouse temperature at the time of germination in the early spring is normally 65° F (18° C). Desert plants are placed on benches near the exhaust fans to take advantage of the warmer temperatures in those areas of the greenhouse. Temperatures near the exhaust fans are usually 10 to 15 degrees warmer than temperatures near the intake.

DISEASE PROBLEMS

Diseases are rarely a problem on sagebrush or rabbitbrush when grown as summer crop. However, <u>Botrytis</u> infections occasionally occur, especiall in the early spring when plants are dense and do not dry out before nightfall. Under these conditions, we regularly spray every 2 weeks with one of the following three fungicides on a rotating basis: Benlate, Ornalin, and Rovral. Later in the year we do not spray unless we see evidence of infection. One of the primary predisposing factors of <u>Botrytis</u> in sagebrush is the indeterminate germination that is so common in this species. Normally plants are thinned approximately 1 month after seeding, but they also need to be thinned a second time several weeks later. If this is not done, late germinants will produce a layer of lush, spindly growth under the main canopy where the humidity is quite high. <u>Botrytis</u> can easily become established on this later growth and will rapidly move to the larger plants. Sagebrush is the only species that seems to require this second thinning, but improved plant growth and health are well worth the extra time which the operation requires.

COLD HARDENING AND SHIPPING

Plants 4 months old are 8 to 10 inches (20 to 25 cm) tall and ready for hardening. The goal is to reach this stage by mid-August. To harden, the plants are watered heavily to remove nitrogen. They are then transferred to a shadehouse providing 47 percent shade. Once the plants are set outside under shade they are not watered again until they exhibit signs of wilting. At this point, the soil is saturated with water and fertilized using a low nitrogen, high phosphorus formulation of 9-45-15. This process subjects the seedlings to moisture and nutrient shock. The plants are further stressed by the shadehouse environment. Wind, nonoptimum temperatures, and shade all combine to slow the rate of top growth and further the development of roots and stem caliper.

By late September the plants are ready to be shipped. Sagebrush and rabbitbrush are shipped throughout the Western United States. Customers include private nurseries, mining companies, State game and highway departments, as well as several federal agencies. Those plants that are not shipped by late fall are overwintered outside and are shipped in the spring.

We constantly monitor our plants and adjust growing schedules and conditions as we learn more about growing these two species. We have found, however, that the procedures outlined here produce strong, healthy plants that are in prime condition for outplanting.

PRELIMINARY REPORT ON TISSUE CULTURE PROPAGATION OF BIG SAGEBRUSH (ARTEMISIA TRIDENTATA)

Walter M. Neville and E. Durant McArthur

BSTRACT: From a single explant of big sagebrush Artemisia tridentata ssp. vaseyana), 65 shoots ere produced in 140 days using Murashige and koog's medium modified by Linsmaire and Skoog, upplemented with 7.1 x 10^{-6} oz/qt (0.2 mg/L), -benzyladenine, and 2 percent sucrose.

NTRODUCTION

ig sagebrush (Artemisia tridentata) can be ropagated from seed and from cuttings Alvarez-Cordero and McKell 1979). A method of ropagation, more rapid than stem cuttings of a ingle plant, that has genetic characteristics of nterest is in vitro or tissue culture propagation Murashige 1974). A species related to big agebrush, tarragon (Artemisia dracunculus L. var. ativa), has been propagated by tissue culture Garland and Stoltz 1980). To develop a rapid ethod of propagation of big sagebrush, we used he tissue culture method developed by Garland and toltz (1980) for tarragon. We are interested in ig sagebrush propagation because of its ncreasing use in revegetation plantings and otential for genetic improvement (McArthur and lummer 1978; Welch and McArthur 1979).

IETHODS AND RESULTS

eeds of A. tridentata ssp. vaseyana collected at iamond Fork, Utah County, UT, were placed between oist paper towels, placed in a closed container, nd alternately located in a cold 37 °F (3 °C) ark place for about 12 hours and in a warmer 73 F (23 °C) lighted place for about 12 hours. In bout a week the seeds started to sprout.

ne-week-old seedlings were sterilized with a .525 percent solution of sodium hypochlorite (a ne-tenth dilution of Purex bleach) for 10 to 15 inutes and then washed with sterile deionized water. The seedlings were excised using sterile technique into four segments: solitary cotyledons, cotyledons with a 0.04-inch (1-mm) hypocotyl stem, hypocotyl stems, and roots.

The various explants were placed on culture medium consisting of Murashige and Skoog (1962) salts, Linsmaire and Skoog (1965) organics, 6 x 10^{-3} oz/1.057 qt (170 mg/L) $NaH_2PO_4 \cdot H_2O$, 2 percent (w/v) sucrose, 0.7 percent agar (w/v), and 7.1 x 10^{-6} oz/1.057 qt (0.2 mg/L) 6-benzyladenine. The sucrose and tissue culture medium were obtained from KC Biological, Lenexa, KS; the agar (Phytagar) and 6-benzyladenine, GIBCO Labs, Santa Clara, CA; the monosodium phosphate, reagent grade, J. T. Baker Chemical Co., Phillipsburg, NJ. The pH of the medium was adjusted to 5.7 - 5.8. Sucrose and agar were dissolved with heating, 0.17 oz (5 ml) of culture medium was pipetted into 0.68 oz (20 ml) borosilicate glass scintillation vials, and sterilized for 22 minutes in a steam sterilizer.

The cultures were incubated at 64 to 71 °F (18-24 °C) in light from a 27-watt cool-white fluorescent lamp at a distance of 17 inches (43 cm) with a photoperiod of 16 hours light, 8 hours dark.

In 6 weeks of culture only the explant consisting of cotyledon with hypocotyl stem produced shoots. After 140 days of culture and 3 transfers at 4 to 6 week intervals, 65 shoots were produced. By the third transfer the cultures lost vitality, and on the fourth transfer only 30 viable shoots remained.

The decline of the culture could have been caused by not having an optimum hormone concentration or by not dividing and transferring the shoots at durations shorter than 4 to 6 weeks. Other possibilities exist.

In future work, we will explore the effects on the vitality and logarithmic-like growth rate of the cultures of different hormone concentrations and intervals of 3 to 4 weeks (at the beginning of shoot elongation) for the division and transfer of the shoots.

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Third in a series of proceedings of symposia on wildland shrubs, this publication brings together current knowledge of plants belonging to two important genera. Topics addressed by the 54 papers include distribution, systematics, genetics, revegetation and control, animal relationships, ecological relationships, entomology, pathology, and physiology.

KEYWORDS: Compositae, wildland shrubs, sagebrush, rabbitbrush, wormwood, southernwood, tarragon, mugwort, wormseed

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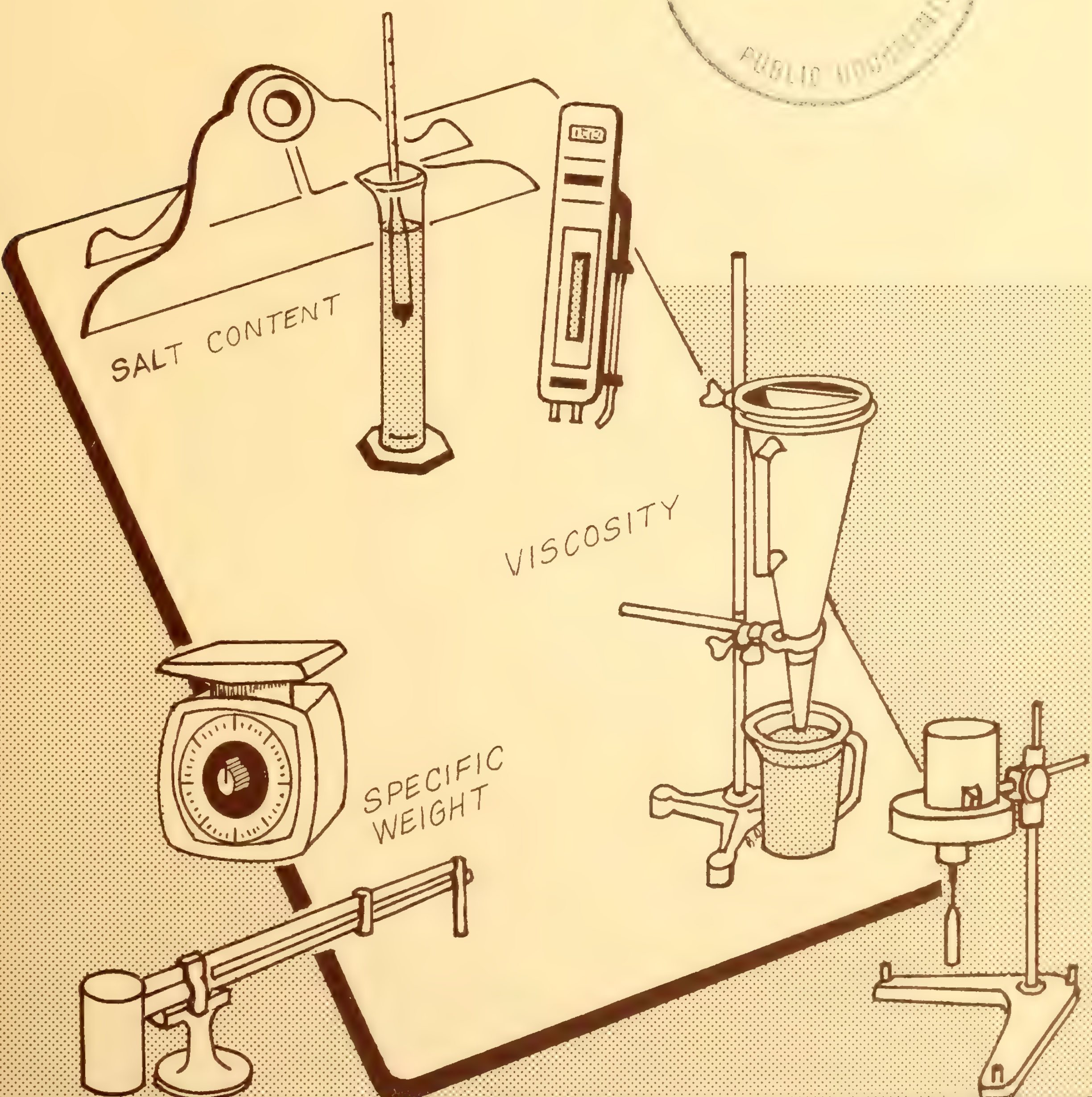
Determining Fire Retardant Quality in the Field

Charles W. George
Cecilia W. Johnson



THE AUTHORS

CHARLES W. GEORGE received his B.S. degree in forest engineering in 1964 and M.S. degree in forestry in 1969. He joined Intermountain Station's staff in 1965 where he has conducted studies related to prescribed fire, pyrolysis and combustion, fire retardants, and aerial delivery systems. Presently Mr. George is Project Leader of the Fire Suppression Research Work Unit at the Intermountain Fire Sciences Laboratory (formerly Northern Forest Fire Laboratory). The current mission of the work unit is to develop the knowledge base and application systems needed to improve fire control capabilities at reduced cost and to facilitate quantitative fire management planning and analysis with emphasis on improving chemical fire suppression technology.

CECILIA W. JOHNSON, a chemist in the Fire Suppression Research Work Unit at the Intermountain Fire Sciences Laboratory, received a degree in chemistry and mathematics from Whitworth College in 1968. She attended graduate school in chemistry at the University of Montana prior to joining the Forest Service in 1971. She works in fire retardant research.

RESEARCH SUMMARY

Wildland fire retardants are evaluated in the laboratory and the field prior to agency approval for operational use. Proper performance requires that the dry c liquid retardant concentrate is mixed with water in th proper proportions and that the properties of the mixed solution remain within prescribed limits until used. To assure this condition, field personnel must have simple and reliable means of measuring the criti cal parameters. Quality of retardants in current use can be ascertained by measuring just two parameters viscosity and active salt content.

Viscosity can be determined by measuring the time required for a specified volume of retardant slurry to flow through the narrow opening (orifice) of a Marsh funnel. Salt content can be determined from the specific gravity (measured by hydrometer) of a thinned retardant. This paper describes the procedures used t measure these properties. Alternate methods using a hand-held density meter, mud balance, and hand-held refractometer are also described. Calibration tables have been developed for most short-term and long-term fire retardants. Some of those included may not be approved for a specific agency's use as a result of varying policies. Also, several retardants used extensively in the past but no longer commercially availabl have been included for baseline references as have several improved formulations that are in final stages of development. In addition to the calibration tables, descriptive information is given on each retardant formulation, sampling techniques, and corrective actions for situations where viscosity and/or salt content are not within acceptable limits.

CONTENTS

Determining Fire Retardant Quality in the Field

Charles W. George
Cecilia W. Johnson

INTRODUCTION

Millions of gallons of forest fire retardants are dropped on wildland fires every year. For both tactical effectiveness and cost effectiveness the retardant must be properly formulated and prepared. Retardants in use have been subjected to laboratory testing wherein the performance of properly mixed retardant is measured and evaluated (USDA Forest Service 1982b,c). Retardant should also be tested in the field to assure that certain critical characteristics are being maintained.

Two specific retardant characteristics that have a major effect on fire control effectiveness and accuracy of delivery are the amount of active retardant chemical (often referred to as salt) and the viscosity (and elasticity) of the prepared slurry. The amount of active salt present is directly related to the retardant's ability to slow a fire. Viscosity (and elasticity) affects the behavior (breakup) of the retardant as it is dropped from an airtanker or sprayed from a ground tanker, and the way it clings together (or breaks apart) and penetrates the fuel complex. Viscosity (and elasticity) is also important in determining the amount of retardant chemical retained on the fuel.

There are a number of methods for determining these important retardant characteristics, but most are not suitable for use under field conditions; that is, they may require elaborate equipment, long time periods, highly trained personnel, or a combination of these and/or other factors.

The retardant-mixing operation at many bases is performed by employees who may have limited knowledge of chemistry and who are often detailed or hired for the job part time. Thus, the field test should not require special skills, should be simple and quick to perform, and should use a minimum of equipment. The tests must give relatively accurate and repeatable results when used by field personnel following detailed procedures.

Previous studies have led to field procedures for determining retardant solution viscosity (George and Hardy 1966, 1967, 1969; George and Johnson 1976) and salt content (George 1971), and have been combined in a guide for field quality control by the Fire Chemical Working Team of the National Wildfire Coordinating Group (1981). The procedures selected for field analysis of salt content were based on correlations of direct salt content measurements made in the laboratory with measurements of specific gravity of the retardant slurry using a hydrometer. Reducing solution viscosity is required with some formulations. The elasticity of fire retardant solutions cannot be readily measured in the field; however, a method of measuring viscosity using a Marsh funnel has proven to be adequate for field characterization of retardants with known rheology.

Since the original procedures and reports incorporating calibration data were published, a number of the retardant formulations have been modified, several are no longer commercially available as originally formulated, and new products have and are being developed. This report describes many short-term and long-term fire retardant products, their physical-chemical properties, and step-by-step procedures and instructions for measuring retardant properties in the field. *Some of the retardants included in the report may not be approved for a specific agency's use as a result of varying policies. Several retardants used extensively in the past but no longer commercially available are included for baseline reference as are several improved formulations that are in final stages of development.* Calibration and conversion tables for each product are included in this paper.

Table 1 summarizes the physical-chemical characteristics and mix ratios of the products discussed in this paper. These are the characteristics of a *properly formulated and mixed* retardant, and although minor deviation can be expected for a number of reasons, major deviation from the values given for either salt content or viscosity for a *properly mixed* retardant suggests a formulation and/or product stability problem. Such variations in operational field mixtures can adversely influence retardant effectiveness and efficiency in fire control operations.

Table 1.—Fire retardant mix factors and characteristics (80 °F)[1]

Retardant	Type of salt[2]	Normal use[3]	Recommended use level lb (gal)/ gal H_2O	Increase in volume	Quantity of powder or concentrate per gal of mixed retardant	Gallons of mixed retardant per ton of powder or concentrate	Specific weight of mixed retardant	Viscosity of mixed retardant	Specific gravity of treated retardant	Percent salt in mixed retardant
			Lb (gal)	*Percent*	*Lb (gal)*	*Gal*	*Lb/gal*	*Centipoise*		
LONG-TERM RETARDANTS										
Unthickened or low-viscosity gum-thickened										
Phos-Chek G-WX	MAP	G	0.96	5.7	0.908	2,203	8.78	<10	1.057	9.6% $NH_4H_2PO_4$
Fire-Trol 934, 936[4]	APP	G	2.95 (0.25)	23.9	2.38 (0.20)	840	9.11	<50	1.100	8.5% P_2O_5
Phos-Chek G-W,G-F,G-R	MAP	G	.96	5.7	.908	2,203	8.78	50-150	1.057	9.4% $NH_4H_2PO_4$
Fire-Trol 931[5]	APP	A	2.99 (.25)	23.6	2.42 (.20)	826	9.15	<50	1.088	8.4% P_2O_5
Phos-Chek 259-F,259-R, 259-W	DAP	A/G	1.14	6.3	1.07	1,869	8.90	50-150	1.068	10.9% $(NH_4)_2HPO_4$
Phos-Chek 259-F,259-R, 259-W	DAP	G	1.60	9.4	1.46	1,370	9.07	50-150	1.089	14.5% $(NH_4)_2HPO_4$
Gum-thickened										
Phos-Chek A-F,A-R,A-W	MAP	A	.96	5.7	.908	2,203	8.78	1,200-1,800	1.057	9.0% $NH_4H_2PO_4$
Fire-Trol GTS-F,GTS-R	AS	A	1.76	10.4	1.59	1,258	9.13	1,200-1,800	1.098	14.8% $(NH_4)_2SO_4$
Phos-Chek D75-F,D75-R, D75-W	AS/MAP	A	1.20	6.9	1.12	1,786	8.91	1,200-1,800	1.071	11.3% $(NH_4)_2SO_4$/ $NH_4H_2PO_4$
Phos-Chek XB	MAP	A	1.14	7.4	1.06	1,885	8.81	1,200-1,800	1.056	10.7% $NH_4H_2PO_4$
Megatard 2700-A										
Liquid sulfate	AS		3.60	22.9	2.93	682	9.71	<10	1.166	28.2% $(NH_4)_2SO_4$
Mixed retardant	AS	A								
Liquid sulfate +			9.71 (1.00)	101	4.83 (.50)	414	9.07	1,200-1,800	1.096	15.0% $(NH_4)_2SO_4$
color/thickener			+.244		+.116	17,241				
Clay-thickened										
Fire-Trol 100	AS	A	2.78	18.2	2.35	851	9.40	1,500-2,500	1.100	15.6% $(NH_4)_2SO_4$
SHORT-TERM RETARDANTS										
Fire-Kill IIP[6]		A/G	.048 (.005)	.4	.048 (.005)	41,667	8.34	150-250	1,000	—
Fire-Trol ST-Poly[7] (Poly-Trol)		A/G	.059 (.006)	.5	.059 (.006)	33,898	8.34	150-250	1,000	—

[1]Consult your agency manuals and guidelines for specific product availability.
[2]Monoammonium phosphate (MAP), diammonium phosphate (DAP), ammonium sulfate (AS), ammonium polyphosphate (APP).
[3]A = aircraft, G = ground.
[4]Specific weight of concentrate is 11.78 lb/gal.
[5]Specific weight of concentrate is 11.96 lb/gal.
[6]Specific weight of concentrate is 9.67 lb/gal.
[7]Specific weight of concentrate is 9.54 lb/gal.

RETARDANT SAMPLING FOR QUALITY CONTROL TESTING

Although the reason for sampling (lot acceptance, routine quality control, or suspected problem) will affect the manner in which a sample is taken, certain general guidelines (see procedures 1 and 2) will usually apply.

1. *Is the sample representative of the product being tested?* Using a sampling valve, a valve at the pump, or sampling from the end of a loading hose may be acceptable in many circumstances. If attempting to sample the retardant in a tank, be sure the contents are circulated adequately to resuspend any settled material and that the sampling point will provide representative tank material. For example, a sampling outlet may contain product from the last sample taken, or a loading hose may contain aged material or material affected by temperature or contamination and therefore no longer representative of the tank contents. A seldom-used outlet low on the tank may sample only the dregs of a prior season's use. If possible, allow the product to flow through or circulate through the sampling outlet for a short time prior to sampling to obtain a representative sample. Discarding 1 gal of retardant that has flowed through a small valve prior to sampling is usually sufficient to obtain a representative sample. A sample taken immediately after recirculation or after filling an aircraft (if a loading valve is used) is usually adequate.

2. *How often should sampling be done?* Samples for lot acceptance testing should be taken from each new truckload (or lot) of retardant as soon as it is received. Testing should also be done during mixing operations. The type of retardant and mix setup will determine the frequency of sampling. For a product that does not require storage, samples should be taken often enough to assure proper adjustment of equipment and maintain product quality. During slow times and early in the year, each airtanker load should be tested. Once equipment is adjusted and personnel are familiar with the operation or when large quantities of retardant are being pumped, samples should be taken periodically (every few hours or no less than daily) during the operations.

Samples can be marked to identify when they were taken (or aircraft loaded) and held for analysis at the end of the day, depending on the purpose of the sampling; however, this does not allow adjustments in retardant quality or equipment settings to be made when needed. In a continuous-mix operation, such as an eductor and silo of retardant, testing should be frequent enough to assure proper concentration (ratio of water to dry retardant). Recirculation is necessary to get a uniform sample. A batch mixer needs less frequent checking (assuming proper formulation of each batch container by the manufacturer and accurate water level indicator). During initial mixing at the beginning of the season every batch should be sampled to assure correct adjustment of the equipment, then periodically during the fire season and several times a day when large quantities are being mixed. Samples are most easily taken from a batch mixer by installing a small valve in the mix tank at about the midpoint of the retardant solution.

Additionally, retardant in storage at a base should be sampled approximately once a week during the fire season. If problems are noticed, such as a change in salt content or loss of viscosity, samples may need to be taken more often. When a base is first opened for the season any material stored over the winter should be tested prior to use. In general, testing should be performed after thorough recirculation; however, if a visual check (or spot sampling) reveals significant stratification in the tanks the supplier should be consulted for specific instructions. (These may include pumping the water layer and about an inch of retardant out of the tank prior to recirculation. The nearly clear layer on top may be condensation or water that has entered the tanks over winter and may be contaminated with bacteria that could cause significant viscosity loss if the water layer were mixed with the remaining retardant.)

3. *Is the sample liquid or dry?* Liquids may be recirculated to resuspend any settled or crystalized material and assure a homogeneous mixture prior to sampling. This is not true of dry products. It is extremely difficult to assure a uniform sample from a complete container of dry materials; however, in many cases, a sample of properly mixed liquid made from dry product provides a good sample if it is properly mixed into a relatively clean, empty tank. This is also true of samples taken for lot acceptance and quality assurance. If a dry sample is required, special care must be taken to obtain a homogeneous sample; it is probably best to request assistance from agency specialists or the manufacturer since there are special techniques and sampling equipment that must be used to obtain a representative sample from a lot of dry material.

4. *Why is this test being performed?* If the sample is to be taken for lot acceptance tests, it is necessary to obtain a uniform sample that is representative of the lot. This will necessitate a relatively clean, empty storage or mix tank to prepare the sample. (See USDA Forest Service 1982a, Lot Acceptance and Quality Assurance Procedures . . .) If the sample is for routine quality control, a sample should be taken after thorough recirculation of the retardant solution to assure a uniform solution. If recirculation between tanks is not possible, then a sample of the contents of each tank should be taken. If the sample is being obtained to troubleshoot a problem (separation, loss of viscosity, etc.), it may be more meaningful to obtain individual samples from throughout the system (top of tank, bottom of tank, loading hose) prior to recirculation in order to identify the source of the problem.

ACTIVE SALT CONTENT

Long-term, combustion-retarding effectiveness of a retardant is related to the type and amount of active chemical, usually referred to as "active salt," that it contains. All salts are not equally effective when applied to fuels in the same concentration. By adjusting the amount of salt in the concentrate or dry product, and the mix ratio or use level, the retardant manufacturers have produced fire retardant formulations with similar combustion-retarding effectiveness. The effectiveness of

the mixed retardant solution is thus directly related to its concentration of the active salt. It is therefore important to maintain the salt content within prescribed limits.

The specific gravity of a retardant solution is directly related to the concentration of retardant salt in the solution. Corrosion inhibitors, coloring agents, flow conditioners, and other ingredients have a minor effect on specific gravity because they are present in relatively low concentrations. Because proportions and quantities of all ingredients in a properly formulated retardant concentrate are relatively constant, the specific gravity of its solutions can be related to the amount of active salt present (George 1971), using conversion tables. But use of specific gravity to determine salt content has limitations. One cannot tell what salt is used, only its quantity. Similarly, when a retardant contains a combination of salts (the relative weights of each must be specified by the manufacturer) the specific gravity method will not indicate whether the proportions of the salts are changed or if one of the salts is missing entirely, merely the total weight of salt. Quantitative laboratory analysis may be necessary to resolve problems of this type.

A procedure has been developed for determining the salt content in the field using a hydrometer and specific gravity/salt content correlation tables. (A hydrometer is a weighted and sealed glass bulb calibrated to be read in specific gravity units.) After the hydrometer is allowed to settle into a solution for several minutes, the specific gravity scale can be read at the liquid meniscus (the lowest point of the curved upper level of the liquid). If the solution has a viscosity appreciably greater than that of water, however, the buoyancy of the hydrometer may give a false reading. In some instances, it is necessary to correct for, minimize, or eliminate this effect by reducing viscosity to less than 200 centipoise. This can be accomplished in several ways, depending on the nature of the thickening agent. For retardants containing clay, such as Fire-Trol 100 or undiluted Fire-Trol 931, the mixed retardant must be filtered to remove the clay before the specific gravity of the clear filtrate is determined. A different procedure for gum-thickened retardants has been developed. Gum-thickened retardants are chemically thinned by adding a "viscosity-reducing agent" (usually an enzyme that when added to the retardant sample causes the thickener to "break" or thin) prior to determining the specific gravity. Special care must be taken to ensure that the viscosity reducing agent and any retardant containing it are properly disposed of because a small amount may thin the contents of an entire storage tank. The equipment necessary to determine salt content in the field is shown in figure 1.

Two other factors must be considered when determining salt content from specific gravity—hydrometer accuracy and solution temperature. The accuracy of the hydrometer in general use varies and occasionally has been found to cause significant errors in retardant quality determinations. Hydrometers with unspecified accuracy should be checked using a known solution. Consistency in handling the hydrometer and the solution each time a reading is taken will minimize inaccuracies. It is recommended that the hydrometer be slowly immersed until the buoyancy supports it in the solution; then the hydrometer should be allowed to settle for to 5 minutes before reading.

All data presented in this paper were gathered at [illegible] °F (26.7 °C). A correction should be made if the temperature varies from the standard. The rule for temperature correction is:

> For every 5 °F (2.8 °C) that the temperature is lower than 80 °F (26.7 °C), subtract 0.001 from the hydrometer reading; for every 5 °F (2.8 °C) that the temperature is greater than 80 °F (26.7 °C), add 0.001 to the hydrometer reading. The corrected hydrometer reading is the value to use to determine salt content.

A table of values to correct for temperatures deviating from 80 °F using the above rule is given in appendix 3, table 26.

The tables for specific retardants are arranged by type of thickener or characteristics:

(a) unthickened or low viscosity gum-thickened (not requiring viscosity-thinning treatment)
(b) gum-thickened
(c) clay-thickened.

The right-hand portion of each retardant/salt table lists "corrections per 100 gal of retardant solution." These values will enable field personnel to adjust the salt content of the retardant if it varies significantly (indicated by the boxed area) from the proper value.

Specific procedures for sampling and determining retardant salt content for each type of product are given in the back of this publication. An alternative to using a hydrometer to determine specific weight of a retardant is to use a hand-held density meter. Although density meters are relatively expensive ($1,000 to $1,500) and are fairly delicate, with care it is possible to use them in the field for quality control measurements. The density meter measures the actual density of the solution including incorporated air. To obtain densities suitable for use with salt content tables the sample must be allowed to sit until the entrapped air has escaped. A hand-held density meter (Mettler DMA-35) is shown in figure 2. Directions for using a hand-held density meter to determine specific weight and salt content are described in procedures 11 and 12 of this paper.

Another alternative to the hydrometer/specific gravity method to determine salt content is the hand-held refractometer. The refractometer is moderately priced (about $150) and has several advantages. Pretreatment of the retardant sample is required only for undiluted liquid concentrates. Temperature corrections are not needed if solution temperatures are between 45 and 100 °F. However, the refractometer may give inaccurate results if it is subjected to extremes of temperature. Low temperatures cause greater changes than do high temperatures. Keep the refractometer between 60 °F and 85 °F for best results. Because the refractometer used for this work incorporates an arbitrary scale, calibration tables developed for this specific instrument are required.

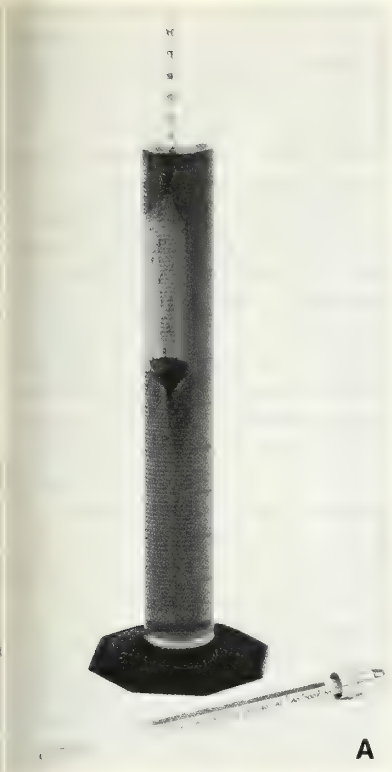


Figure 1.—Equipment for determining salt content: (A) unthickened or low-viscosity retardants; (B) gum-thickened retardants; (C) clay-thickened retardants.

Figure 2.—Hand-held density meter (Metler DMA-35).

Procedure 13 describes the use of the refractometer and provides tables for determining retardant salt content with the refractometer, American Optical Scientific Instruments, Model 1440, shown in figure 3.

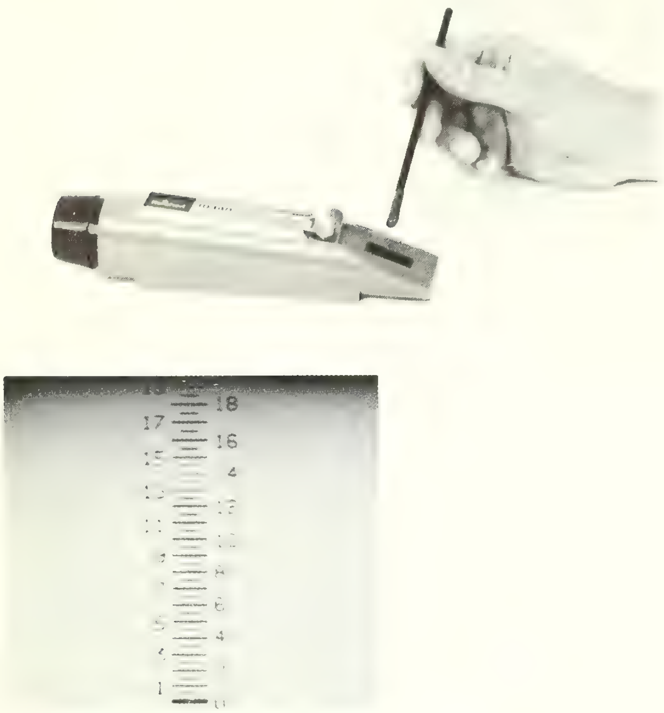


Figure 3.—Refractometer (American Optical Scientific Instruments, Model 1440).

VISCOSITY

The physical-chemical or rheological properties of a retardant slurry have a major impact on the delivery, distribution, accuracy, and effectiveness of a retardant drop (George 1981). The viscosity of the retardant solution is the most common rheological property used to characterize retardant performance because it is easily measured. The performance of a particular retardant, however, is dependent on several rheological properties rather than just viscosity; that is, the retardant with the highest viscosity does not necessarily have the best drop characteristics and performance.

As the retardant leaves the aircraft, droplets are stripped from the falling mass of retardant by the air velocity acting on it. This stripping action, often referred to as breakup, is affected by the cohesiveness of the retardant (resistance to breakup). The cohesiveness is determined by the rheological properties, including viscosity. It is known, however, that the elasticity (another rheological property) of the solution is the most important property affecting breakup (Andersen and others 1974a, 1974b). Too little elasticity of the retardant solution, such as in the case of water or unthickened retardants, results in little resistance to breakup and causes a mistlike condition where most of the retardan occurs as very small retardant droplets. Small droplets evaporate faster, are influenced more by wind, and result in less retardant being spread over a larger area. Accuracy is more difficult because crosswinds may blo clouds of small drops beyond targeted areas.

Rheological properties (including viscosity and elasticity) also affect the ability of the fire retardant to remai on the fuel and spread over the fuel surface (combustio retarding effectiveness is related to the amount of fuel surface covered with retardant). That is, how much of the retardant coming in contact with the fuel will adhe to it to build up a retardant coating, and how much wi run or drip off, either to come into contact with lower aerial fuel or the ground? The extent to which differences in retardant thickening systems may affect retention of retardant by aerial fuels and the fuel coating characteristics has not been well defined. Previous studies have indicated that the overstory can intercept significant portion of the retardant dropped. Actually, the difference between amounts of thickened and unthickened retardant reaching the ground below the overstory was small (less than 6 percent) (Johansen and Shimmel 1967). Recent studies conducted in Australia (George 1984) indicated that in eucalyptus fuels, gum- and polymer-thickened retardants performed better tha unthickened when both the ability to penetrate the overstory and to coat aerial fuels are considered. Retention by the aerial fuels was somewhat greater with thic ened retardant, as expected; however, contrary to common belief, so was the amount reaching the ground. (Less retardant was lost to evaporation and drift and there was less dispersion, especially before the retardan cloud entered the overstory.) There were larger areas of the higher coverage levels that more than made up for differences in canopy interception. Thus, the impact of differences in the rheology of different thickening agent in terms of retardant penetrating an overstory is only a fraction of the retardant losses due to evaporation and drift occurring during a retardant drop.

The use of standard and consistent products will allo experienced fire personnel to accurately predict the behavior of specific retardants and adjust for retardant type when planning a fire control strategy. If the retardant being used fails to act in the expected manne that strategy may fail.

Measurement of the rheological properties necessary t specify a retardant's performance is difficult because of the relative importance of the specific properties (viscosity, elasticity, etc.) and the interactions that occur between them in the case of each general type of retardant. Although elasticity might be a better measur of retardant performance than viscosity, it is difficult to measure, both in the laboratory and field. Viscosity, on the other hand, can be easily measured in the laboratory or field. To achieve acceptable results, only a few conditions of the measurements need to be held constant or monitored. Each retardant formulation has specific rheological properties that vary with thickener concentration (mix ratio). Thus retardant viscosity can serve as an indicator of performance for a given retardant formulation with known rheological properties.

The viscosity of fire retardants has generally been measured using a Brookfield viscometer (model LVF) (fig. 4). The Brookfield viscometer rotates a cylindrical spindle that is immersed in the fluid for which the viscosity is to be determined. The spindle is rotated at a selected speed and the viscous drag exerted by the fluid on the motor is measured. For a reference or standard, a spindle speed of 60 r/min is used with either spindle 2 or 4, depending on the viscosity of the solution (spindle 2 for viscosities below 500 cP or spindle 4 for viscosities above 500 cP). Use of a different speed setting will result in a different viscosity reading, because the relationship of shear rate (r/min) and viscosity are nonlinear for such products. Procedure 7 contains directions for measuring viscosity using the Brookfield viscometer.

The most accurate retardant viscosities will be obtained if samples are not tested until hydration of the thickener is complete and most entrapped air is released. Hydration and release of air bubbles can take from 15 minutes up to 1 hour, depending on mixing and recirculation time, and depending on the specific hardware and situation. The Brookfield viscometer has not been incorporated in field operations, probably because of the cost of the instrument (about $800) and its delicacy.

As an alternative to the Brookfield viscometer, the viscosity of a retardant slurry can be related to the time required for a fixed quantity of slurry to flow through a small hole of known diameter and length. The Marsh funnel (designed for determining the viscosity of drilling muds) has been adapted for this purpose (George and Hardy 1966) and is shown in figure 5. (Instructions for converting a Marsh funnel and commercial sources are available from Intermountain Fire Sciences Laboratory, P.O. Box 8089, Missoula, MT 59807.) The Marsh funnel is filled with retardant and the time for 1 quart to flow through determined. (See procedure 8 for details.)

Figure 4.—Brookfield viscometer used to determine retardant viscosity.

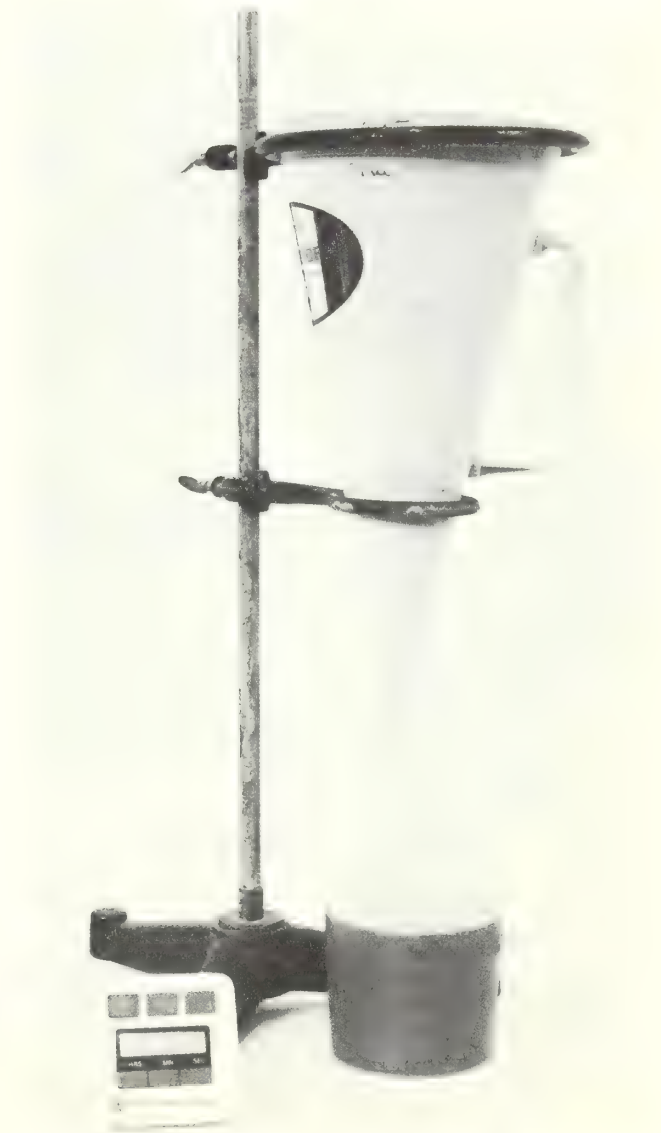


Figure 5.—Marsh funnel used for determining retardant viscosity.

Table 22 (see procedure 8) relates Marsh funnel time to retardant solution viscosity as measured with the Brookfield viscometer. The Marsh funnel time read to the nearest second and compared to table 22 will give viscosities accurate to ±200 centipoise (±10 percent). Such accuracy is adequate for field use. Because thickened retardants are suspensions rather than true solutions measurements of both Marsh funnel time and Brookfield viscosity vary considerably. The retardant concentration, temperature of the solution, time since agitation or recirculation, and age of retardant can affect the viscosity. The tabulated values apply only to the viscosity at the time and temperature of measurement. As the temperature of a retardant solution increases, the viscosity decreases. Conversely, as the temperature of a retardant solution decreases, the viscosity increases. For this reason temperature should be noted as well as the Marsh funnel flow-through time. A material that is too thin at 90 °F may be adequate at 80 °F.

The diameter of the orifice of the Marsh funnel should be 0.269 ± 0.002 inch for the large tip and 0.187 ± 0.002 inch for the small tip. Variations between Marsh funnels in the orifice diameter and length, and volume will cause variations in flow-through time. These variations may result in different viscosity determinations when different funnels are used. Nevertheless, this variation is not usually a problem if it is remembered that Marsh funnel viscosities are accurate to about ±200 centipoise (±10 percent) for most thickened products.

Specific tables were developed using freshly mixed retardant that was fully hydrated and contained a minimum of entrapped air. The length of storage time and degree of agitation prior to sampling may affect the results.

The viscosities of unthickened, diluted Fire-Trol 931-L, 934-L, 936-L, and Megatard 2700 (liquified sulfate) are very low and limit the usefulness of the Marsh funnel. The Brookfield viscosity for Fire-Trol 931-L is approximately 70 centipoise, while the viscosities of Fire-Trol 934-L and 936-L and Megatard liquified sulfate are approximately 10 centipoise.

Because adjusting the viscosity is not as straightforward as adjusting the salt content, changes are not often undertaken unless deviations are excessive. General methods are discussed under the section "Taking Corrective Action." Severe or continued problems in achieving a proper mix should be reported to the agency specialist or other authority and the manufacturer.

SPECIFIC WEIGHT

The specific weight of a retardant is the weight of 1 gal of the mixed retardant, typically expressed in pounds. Although specific weight is usually less accurate an indication of salt content than the other measurements, the specific weight of a sample can be an indicator of whether or not the retardant is properly mixed. It is imperative that entrapped air has been removed. Variations from the acceptable levels should be verified by performing the salt content test before corrective action is taken. Determining the specific weight of a highly aerated retardant can, however, be useful for applications such as determining the actual weight loaded onto an airtanker. Procedures 9, 10, and 11 give detailed instructions for determining the specific weight of a retardant using conventional weight/volume measurements, a mud balance, and a hand-held density meter (fig. 2). A mud balance is shown in figure 6.

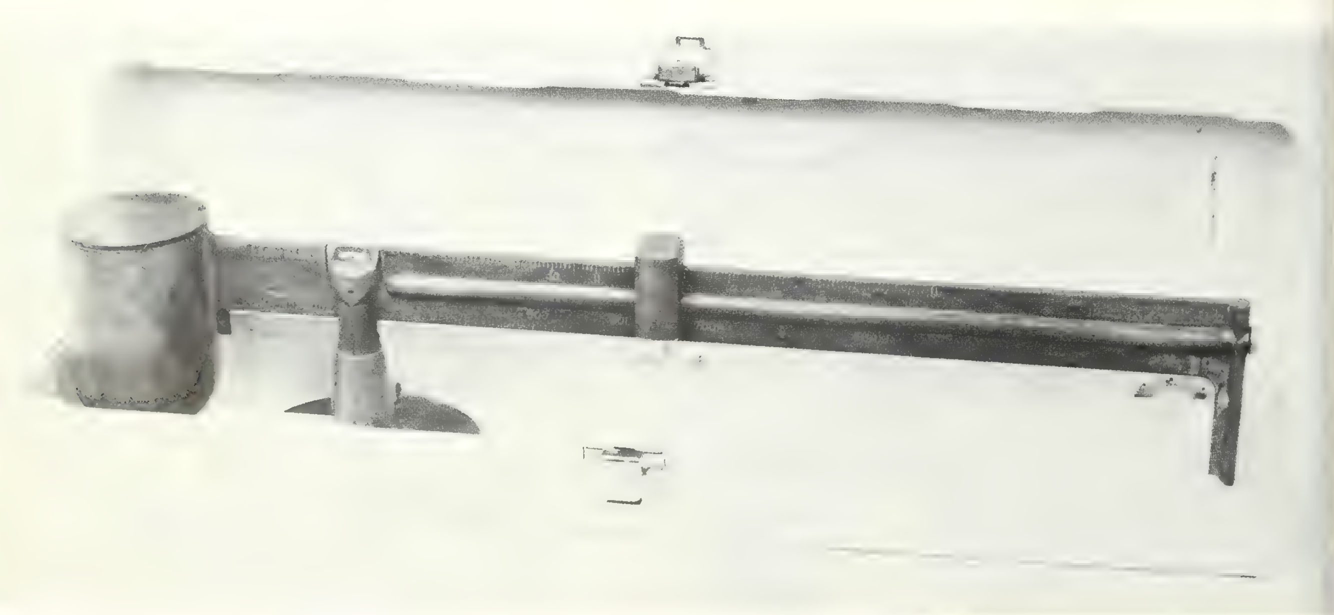


Figure 6.—Mud balance used to determine the specific weight of a retardant.

TAKING CORRECTIVE ACTION

When should corrective action be taken? During the fire season retardant solutions not meeting acceptable characteristics should be corrected as soon as detected. All the tables indicate ranges that will yield acceptable performance and allow some leeway for normal variation in manufacturing and mixing.

If a problem has occurred during the off season, consult the manufacturer and agency experts. Some corrective procedures recommended for use during the fire season may aggravate a problem during winter storage of retardant solution.

An improperly mixed product can cause many problems. If the values are above those specified, the retardant may:

1. Contain excessive salt and cost more per gallon than necessary.
2. Be too viscous to flow readily in loading operation.
3. Salt-out or precipitate in storage, especially as temperatures fluctuate.
4. Exhibit abnormal drop characteristics.
5. Cause excessive corrosion.

If the test values are lower than those specified, the retardant may:

1. Not effectively retard the fire because of inadequate salt content.
2. Experience greater losses due to evaporation and wind drift when dropped from an airtanker.
3. Separate easily in storage.
4. Be more susceptible to viscosity loss and more corrosive due to inadequate levels of bactericide and corrosion inhibitors.

What corrective action should be taken? The corrective action to be taken depends on the characteristics of the particular retardant. The following guidelines are generally appropriate for correcting deficiencies found during the fire season and are based on the type of retardant.

The most common quality control problem is improper mixing ratio leading to other than recommended salt content and viscosity and possibly inadequate short-term stability. The basic corrective action is to adjust the amounts of water and/or retardant concentrate in the mixed retardant.

If both salt content and viscosity are high, water can be added to the slurry using the salt content tables as a guide and thoroughly recirculating the stored retardant. The salt content tables show the amount of water or retardant concentrate per 100 gal of slurry necessary to achieve the proper salt content.

If both salt content and viscosity are low, it is necessary to add retardant concentrate (dry or liquid) to the mixed retardant to obtain the proper level of salt and viscosity. This can be accomplished in several ways, depending on the retardant and particular mixing and storage facilities (each base should develop procedures suitable to the retardant and equipment used). The total amount of additional dry retardant or liquid concentrate required should first be calculated using the correction factors provided. For liquid concentrate formulations, the concentrate can simply be added and the entire mix thoroughly recirculated. This, however, is an infrequent situation, because retardant mixed from liquid concentrates is seldom stored (for aerially applied retardants), but instead it is pumped directly into the aircraft. Suitable adjustments to the proportioning equipment should be made and verified. In the case of dry retardant formulations where quantities of mixed retardant are stored, the corrective action depends on the amount of dry product to be added. In some cases, it will be possible to mix a particularly rich (more powder or less water than usual) batch of retardant and add it to the product in storage, and then recirculate. In other cases, especially with the lower viscosity products or when only a slight correction is needed, the additional dry powder may be added to the stored retardant directly in a batch mix or by passing retardant slurry rather than water through an eductor mixer, while drawing additional powder. In all cases, the stored retardant should be recirculated very thoroughly and then retested. The time required for recirculation depends on the specific storage and handling system. To estimate the time to turn the stored retardant once, divide the total stored retardant by the pumping rate. For example, a 10,000-gal tank of mixed retardant should be recirculated for at least 25 minutes if the pumping capacity is 400 gal per minute (10,000 gal $\div$ 400 gal/min = 25 min). Adequate recirculation should be achieved if pumping is continued for about four times this duration. Although this is not possible in all situations, the longer the recirculation time, the more uniform the solution throughout the tank, and the more accurately the test results will reflect the true situation.

If the salt content is low and the viscosity is high, the problem is more difficult to correct. This is a rare situation and usually occurs with clay-thickened retardants or gum-thickened retardant mixed with unusually cold water. (The viscosity of clay-thickened retardants will increase with increased shear or mixing time; thus relatively high viscosities can be produced at nearly any salt content.) In the case of clay-thickened retardant, the salt content should be corrected first. Usually adding a batch or two of retardant mixed on the rich side and recirculating will correct the salt deficiency. For clay-thickened retardants, the additional batch should be mixed with the minimum shear that will yield a stable slurry. This will aid in lowering the viscosity. With a gum-thickened product (normal mixing-water temperatures), the viscosity cannot be adjusted easily and will likely remain high. Recirculate the tank thoroughly (a very high viscosity solution tends to form a separate layer rather than mix with other solutions), or if possible, circulate to mix several tanks together. This will improve mixing and allow greatest possible lowering of viscosity. The viscosity of gum-thickened retardants usually peaks at some period (12 to 36 hours) after mixing, depending on the specific mixing procedure and equipment. If operations allow, it is recommended that a further sample or samples be taken after this time has elapsed. Prior to any adjustment be sure to consider the temperature of the retardant and whether it is likely to change in storage. It is recommended that adjustments be made to obtain the proper salt content and the resulting viscosity be accepted unless extremes exist. If this occurs, assistance from the agency technical staff and the manufacturer should be sought.

If the salt content is high and the viscosity is low, the addition of a "lean" mix or water (depending on the situation and equipment available) will correct the salt content. It is recommended that a slightly high salt content (10 to 15 percent above the normal acceptable range) be used if additional corrections mean lowering further a substandard viscosity. For a clay-thickened retardant, such as Fire-Trol 100, additional shearing (longer mix time) will raise the viscosity, as previously discussed. On the other hand, the viscosity of gum-thickened retardants cannot be controlled independently of the salt content and there are a limited number of things that can be done to adjust the viscosity. An additional viscosity test may be appropriate for a freshly mixed batch, as other factors such as water temperature will affect the rate of hydration (viscosity development). Although a low viscosity may alter the drop characteristics, separation of the mixed product is also possible. This may lead to compounding problems and result in an increased loss of the viscosity. If possible, storage of such retardant in a separate tank and/or prompt use are recommended. Remember that a properly mixed retardant that loses its viscosity may still be an effective retardant and perform similarly to unthickened or waterlike retardants.

A gum-thickened retardant held in storage for long periods of time can be expected to show some loss of viscosity due to deterioration. Loss of viscosity of freshly mixed retardant or retardant stored for only a short time is also possible and may be a result of contamination. Examples of contamination are:

1. Enzyme - either the viscosity-thinning agent (breaker) used for the salt content test or enzymes from natural bacteria. A very dilute solution of retardant such as would occur after incomplete rinsing and emptying of a mix tank (or if the mix tank is routinely filled with water for the next batch immediately after emptying and without cleaning) is an excellent growth medium for bacteria, and if allowed to sit for several days or weeks, bacterial growth could be sufficient to overwhelm the bactericides in the retardant formulation. There are also many natural sources of bacterial contamination occurring in the air and water used for preparing the retardant. Bacteria from all these sources produce enzymes that may degrade the retardant.
2. Excessive amount of chlorine. Bleach used for disinfection is a potential source of chlorine contamination. Tanks treated with chlorine must be thoroughly rinsed prior to use with retardant.
3. Oil, gas, brighteners, or other chemicals found around bases and aircraft.
4. Other types of retardant.

Viscosity is not generally a concern for unthickened o slightly thickened materials. In most cases, it is not necessary to develop correlations between Marsh funnel times and viscosity. In those instances where correlations can be used (Phos-Chek 259 and G series of retardants), however, they have been included. Adjustin salt content to the proper level by addition of water or additional retardant powder or concentrate on the low-viscosity products is sufficient in most cases.

In all cases, the effect of temperature should not be overlooked. In general, the higher the temperature of th solution, the faster the viscosity of the retardant will deteriorate if any of the above factors are present.

RECORDKEEPING

It is recommended that each retardant-mixing base maintain permanent quality control records that include data on each lot of retardant received, retardant sent to other locations for testing, and tests performed at the base. Appendix 5 offers examples of recordkeeping form that include information for assessing retardant quality.

When a lot (usually a truckload) of retardant is received, enough information should be recorded to assure future identification. This would include date and time of receipt, quantity of product received, manufacturer's lot number, and invoice or freight bill number.

When a sample is sent to another location for testing (for lot acceptance or to manufacturer for troubleshooting), a record should be made of date and location shipped, manner of sampling, date and time mixed, results of tests performed at the base, lot identification, and reason for sending the sample.

Results of all base tests should also be kept, including mixing and sampling dates and times, solution temperatures, Marsh funnel times and corresponding viscosities, specific gravity and corrections to the specific gravity, and the corresponding salt content. Product identification to the extent known should be included as well as the reason for testing (routine quality control, troubleshooting, etc.). Additional information, such as sampling location (top, tank 1; loading hose pumping from tank 2; etc.) and when tank was last recirculated o new product added, is often helpful as well.

These records are useful when monitoring product quality trends and provide essential background when documenting incidents involving retardant performance and application.

LONG-TERM RETARDANT FORMULATIONS

Unthickened or Low-Viscosity Gum-Thickened Retardants

Phos-Chek® G-WX.—Phos-Chek G-WX is a monoammonium phosphate-based retardant formulation containing no color or thickener (G-ground, W-white, X-no thickener), and designed for ground application. Phos-Chek G-WX contains corrosion inhibitors and can be mixed by an eductor system, batch-mixed, or put in solution by recirculation with water. In other respects, the formulation is like Phos-Chek A and G.

Application	: Ground tanker and helicopter bucket.
Use level	: 0.96 lb of dry retardant mixed with 1 gal of water will produce 1.057 gal of mixed retardant. Each gallon of mixed retardant contain the equivalent of 0.908 lb of powder.
Viscosity	: <10 centipoise (cP).
	: Field measurement for viscosity is not meaningful; therefore, no data are provided.
Salt content	: 9.6% by weight MAP ($NH_4H_2PO_4$).
	: Field measurement (hydrometer): a reading of 1.057 at 75 °F (procedure 3 and table 2 for conversion to salt content and acceptable range).
Specific weight:	8.78 lb/gal slurry (procedure 9, 10, or 11).

Phos-Chek® G-W, G-R, and G-F.—Phos-Chek G-W, G-R, and G-F are monoammonium phosphate-based retardant formulations designed for application from the ground or helicopter bucket. Phos-Chek G-W is uncolored (W-white), while G-R contains iron oxide coloring (R-red), and G-F contains a fugitive coloring agent (F-fugitive). (Fugitive coloring agents fade to a neutral shade several weeks after application.) Phos-Chek G-W, G-R, and G-F contain a low concentration of gum-thickener to provide viscosity in order to improve retardant drop characteristics and adherence to the fuel. The products also contain bactericide and corrosion inhibitors.

Application	: Ground tanker and helicopter bucket.
Use level	: 0.96 lb of dry retardant mixed with 1 gal of water will produce 1.057 gal of mixed retardant. Each gallon of mixed retardant contains the equivalent of 0.908 lb of powder.
Viscosity	: 50-150 centipoise (cP).
	: Field measurement (Marsh funnel): 35-50 sec through the small tip (procedure 8 and table 22 show conversions to viscosity and acceptable range).
Salt content	: 9.4% by weight MAP ($NH_4H_2PO_4$).
	: Field measurement (hydrometer): a reading of 1.057 at 80 °F (procedure 3 and table 2 for conversion to salt content and acceptable range).
Specific weight:	8.78 lb/gal slurry (procedure 9, 10, or 11).

Table 2.—Salt content of Phos-Chek G-WX, G-W, G-R, and G-F related to specific gravity at 80 °F (use with procedure 3)

Measured specific gravity of the retardant	Percent by weight $NH_4H_2PO_4$	Percent by weight P_2O_5 equivalent	Correction required per 100 gallons of retardant solution: Retardant	Correction required per 100 gallons of retardant solution: Water
			Lb	*Gal*
1.000	0.5	0.3	91	
1.005	1.3	0.8	84	
1.010	2.1	1.3	76	
1.015	2.9	1.8	68	
1.020	3.7	2.3	60	
1.025	4.5	2.6	52	
1.030	5.3	3.2	45	
1.035	6.0	3.7	36	
1.040	6.8	4.2	28	
1.045	7.6	4.7	20	
1.050	8.4	5.2	12	
1.051	8.6	5.3	10	
1.052	8.8	5.4	9	
1.053	8.9	5.5	7	
1.054	9.1	5.6	5	
1.055	9.2	5.7	4	
1.056	9.4	5.8	2	
1.057	**9.6**	**5.9**	**0**	**0**
1.058	9.7	6.0		2
1.059	9.9	6.1		3
1.060	10.0	6.2		5
1.061	10.2	6.3		7
1.062	10.3	6.4		9
1.063	10.5	6.5		10
1.065	10.9	6.7		14
1.070	11.6	7.2		23
1.075	12.4	7.7		32
1.080	13.2	8.2		41
1.085	14.0	8.7		50
1.090	14.8	9.1		60
1.095	15.6	9.6		69
1.100	16.4	10.1		79
1.105	17.2	10.6		88
1.110	18.0	11.1		98
1.115	18.8	11.6		108
1.120	19.6	12.1		117
1.125	20.4	12.6		127
1.130	21.2	13.1		137
1.135	22.0	13.6		147
1.140	22.8	14.1		157
1.145	23.6	14.6		168
1.150	24.4	15.0		178

The boxed area represents a variation in salt content such that no corrective action is needed.

Fire-Trol® 934-L and 936-L.—Fire-Trol 934-L and 936-L are formulations comprised of liquid ammonium polyphosphate (Arcadian Poly-N® 11-37-0 diluted to 10-34-0), and designed for ground application only. (Poly-N was previously a product of Allied Chemical Co.) Fire-Trol 934-L has no coloring added, and Fire-Trol 936-L contains red dye. These products do not contain a thickener, and the solutions are light in color. A corrosion inhibitor contained in the formulation imparts a bluish tint to the uncolored Fire-Trol 934-L. Both products contain a wetting agent for improved penetration of organic fuels. Fire-Trol 934-L and 936-L can be batch-mixed by dilution and agitation during circulation, or they can be mixed using simple proportioners, eductors, or other devices controlling the flow of the concentrate and water, and relying on flow-induced turbulence or pump-mixing.

Application	:	Ground tanker and helicopter bucket.
Use level	:	1 gal of liquid concentrate mixed with 4 gal of water will produce 4.96 gal of mixed retardant. Each gallon of mixed retardant contains the equivalent of 0.20 gal of liquid concentrate.
Viscosity	:	<50 centipoise (cP).
	:	Field measurement for viscosity is not meaningful; therefore, no data provided.
Salt content	:	8.5% by weight P_2O_5 equivalent.
	:	Field measurement (hydrometer): a reading of 1.100 at 80 °F (procedure 3 and table 3 for conversion to salt content and acceptable range). Field measurement (refractometer): a reading of 16.9 (procedure 13 and table 4 for conversion to salt content and acceptable range).
Specific weight:		9.11 lb/gal slurry (procedure 9, 10, or 11).

Table 3.—Salt content of Fire-Trol 934-L and 936-L related to specific gravity at 80 °F (use with procedure 3)

Dilution ratio	Measured specific gravity of the retardant	Percent by weight P_2O_5	Correction required per 100 gallons of retardant solution: Retardant	Water
			------ Gallons ------	
20:1	1.020	2.1	19.3	
15:1	1.029	2.8	17.3	
10:1	1.045	4.1	13.6	
9:1	1.049	4.4	12.6	
8:1	1.055	4.9	11.2	
7:1	1.062	5.5	9.5	
	1.065	5.7	8.8	
	1.070	6.1	7.5	
6:1	1.071	6.2	7.3	
	1.075	6.5	6.3	
	1.080	6.9	5.1	
5:1	1.084	7.2	4.0	
	1.085	7.3	3.8	
	1.090	7.7	2.5	
	1.095	8.1	1.2	
	1.096	8.2	1.0	
	1.097	8.3	0.7	
	1.098	8.4	0.5	
	1.099	8.4	0.2	
4:1	**1.100**	**8.5**	**0**	**0**
	1.101	8.6		1
	1.102	8.7		2
	1.103	8.8		3
	1.104	8.8		4
	1.105	8.9		5
	1.110	9.3		11
	1.115	9.7		16
	1.120	10.1		21
3:1	1.123	10.4		25
	1.125	10.5		27
	1.130	10.9		32
	1.135	11.3		38
	1.140	11.7		43
	1.145	12.1		49
	1.150	12.5		55
	1.155	13.0		60
	1.160	13.4		66
2:1	1.162	13.5		69
	1.165	13.8		72
	1.170	14.2		78
	1.175	14.6		84
	1.180	15.0		90
	1.185	15.4		96
	1.190	15.8		102
	1.195	16.2		108
	1.200	16.6		114
	1.205	17.0		120
	1.210	17.4		126
	1.215	17.8		133
	1.220	18.2		139
	1.225	18.6		145
1:1	1.229	18.9		151
	1.230	19.0		152
	1.235	19.4		158
	1.240	19.8		165
	1.245	20.2		171
	1.250	20.6		178
	1.275	22.6		212
	1.300	24.6		247
	1.325	26.7		283
	1.350	28.7		320
	1.375	30.7		359
Conc	1.398	32.5		395
	1.400	32.7		399

(con.)

Table 3.—(Con.)

The boxed area represents a variation in salt content such that no corrective action is needed.

ıble 4.—Salt content of Fire-Trol 934 and 936 related to scale reading on the refractometer (use with procedure 13)

lution ratio	Refractometer scale reading for the retardant	Percent by weight P_2O_5	Correction required per 100 gallons of retardant solution: Retardant	Water
			Gallons	
20:1	4.4	2.1	19.1	
15:1	5.6	2.7	17.4	
10:1	8.1	4.0	13.7	
9:1	8.9	4.4	12.5	
8:1	9.7	4.8	11.3	
7:1	11.0	5.5	9.4	
	11.5	5.8	8.6	
	12.0	6.0	7.8	
6:1	12.4	6.2	7.2	
	12.5	6.3	7.0	
	13.0	6.5	6.2	
	13.5	6.8	5.4	
	14.0	7.0	4.7	
5:1	14.3	7.2	4.2	
	14.5	7.3	3.9	
	15.0	7.5	3.1	
	15.5	7.8	2.2	
	16.0	8.1	1.4	
	16.5	8.3	0.6	
4:1	**16.9**	**8.5**	0	0
	17.0	8.6		1
	17.5	8.8		4
	18.0	9.1		7
	18.5	9.3		11
	19.0	9.6		14
	19.5	9.8		18
	20.0	10.1		21
	20.5	10.3		24
3:1	20.6	10.4		25
	21.0	10.6		28
	21.5	10.9		31
	22.0	11.1		35
	22.5	11.4		38
	23.0	11.6		42
	23.5	11.9		45
	24.0	12.1		49
	24.5	12.4		52
	25.0	12.6		56
	25.5	12.9		60
	26.0	13.2		63
	26.5	13.4		67
2:1	26.7	13.5		68
	27.0	13.7		71
	27.5	13.9		74
	28.0	14.2		78
	28.5	14.4		82
	29.0	14.7		83
	29.5	14.9		89
	30.0	15.2		93

ıe boxed area represents a variation in salt content such that no corrective :tion is needed.

Fire-Trol® 931-L.—Fire-Trol 931-L is a formulation composed primarily of liquid ammonium polyphosphate (Arcadian Poly-N 11-37-0 diluted to 10-34-0), and designed for fixed-wing and helicopter bucket air application. (Poly-N was previously a product of Allied Chemical Co.) Although attapulgite clay is added to the concentrate to suspend the color and enhance visibility, when diluted for use it is essentially an unthickened product. Fire-Trol 931-L contains a corrosion inhibitor, and iron oxide and a dye provide the color. Mixing is accomplished through simple proportioning of the retardant concentrate and water. The resulting mixed retardant is usually pumped directly into aircraft without intermediate storage.

Application : Demand-mixed air tanker and helicopter bucket. Can be used for ground application, but less suitable than Fire-Trol 934-L or 936-L.

Use level : 1 gal of liquid concentrate mixed with 4 gal of water will produce 4.94 gal of mixed retardant. Each gallon of mixed retardant contains the equivalent of 0.20 gal of liquid concentrate.

Viscosity : <50 centipoise (cP).

: Field measurement for the viscosity of the retardant mixed 4:1 is not meaningful; therefore, no data provided for the mixed retardant. Viscosities can be determined on the concentrate (procedure 8 and table 22).

Salt content : 8.4% by weight P_2O_5 equivalent.

: Field measurement (hydrometer): a reading of 1.224 at 80 °F for the liquid concentrate (procedure 6 and table 5 for conversion to salt content). A reading of 1.108 at 80 °F for the mixed retardant (procedure 3 and table 6 for conversion to salt content and acceptable range). For more precision, a sample may be filtered prior to reading. A reading of 1.088 at 80 °F for a filtered sample (procedure 5 and table 7 for conversion to salt content and acceptable range).

Field measurement (refractometer): a reading of 15.6 (procedure 13 and table 8 for conversion to salt content and acceptable range).

Specific weight: 9.15 and 11.96 lb/gal, respectively, for mixed retardant and liquid concentrate (procedures 9, 10, or 11).

Table 5.—Salt content of Fire-Trol 931-L concentrate related to specific gravity at 80 °F (use with procedure 6)

Measured specific gravity of the diluted retardant filtrate	Percent by weight P_2O_5
1.150	22.9
1.155	23.5
1.160	24.1
1.165	24.7
1.170	25.3
1.175	25.9
1.180	26.6
1.185	27.2
1.190	27.8
1.195	28.4
1.200	29.0
1.205	29.6
1.210	30.2
1.215	30.8
1.220	31.4
1.224	**31.9**
1.225	32.0
1.230	32.6
1.235	33.3
1.240	33.9
1.245	34.5
1.250	35.1
1.255	35.7
1.260	36.3
1.265	36.9
1.270	37.5
1.275	38.1
1.280	38.7
1.285	39.4
1.290	40.0
1.295	40.6

The boxed area represents a variation in salt content such that no corrective action is needed.

Table 6.—Salt content of Fire-Trol 931-L related to specific gravity at 80 °F (use with procedure 3)

Dilution ratio	Measured specific gravity of the retardant	Percent by weight P_2O_5	Correction required per 100 gallons of retardant solution: Retardant	Correction required per 100 gallons of retardant solution: Water
			---- Gallons ----	
20:1	1.013	2.1	18.9	
15:1	1.023	2.7	17.1	
10:1	1.042	4.0	13.4	
9:1	1.048	4.4	12.4	
8:1	1.055	4.9	11.1	
	1.060	5.2	10.0	
7:1	1.064	5.5	9.2	
	1.065	5.5	9.0	
	1.070	5.9	8.0	
6:1	1.075	6.2	7.0	
	1.080	6.5	6.0	
	1.085	6.9	5.0	
5:1	1.089	7.1	4.2	
	1.090	7.2	3.9	
	1.095	7.5	2.9	
	1.100	7.9	1.8	
	1.101	7.9	1.6	
	1.102	8.0	1.4	
	1.103	8.0	1.2	
	1.104	8.1	1.0	
	1.105	8.2	0.7	
	1.106	8.2	0.5	
	1.107	8.3	0.3	
4:1	**1.108**	**8.4**	**0**	**0**
	1.109	8.4		0
	1.110	8.5		1
	1.111	8.6		2
	1.112	8.6		3
	1.113	8.7		4
	1.114	8.8		5
	1.115	8.8		6
	1.116	8.9		7
	1.120	9.2		10
	1.125	9.5		15
	1.130	9.8		19
	1.135	10.2		24
3:1	1.137	10.3		26
	1.140	10.5		28
	1.145	10.8		33
	1.150	11.2		38
	1.155	11.5		42
	1.160	11.8		47
	1.165	12.2		52
	1.170	12.5		57
	1.175	12.8		62

The boxed area represents a variation in salt content such that no corrective action is needed.

Table 7.—Salt content of Fire-Trol 931-L related to specific gravity of the retardant at 80 °F (filtered for improved accuracy and readability) (use with procedure 5)

Dilution ratio	Measured specific gravity of the retardant filtrate	Percent by weight P_2O_5	Correction required per 100 gallons of retardant solution: Retardant	Water
			----- Gallons -----	
20:1	1.018	2.1	19.2	
15:1	1.025	2.7	17.1	
10:1	1.039	4.0	13.6	
9:1	1.043	4.4	12.5	
8:1	1.048	4.9	11.6	
	1.050	5.0	11.1	
7:1	1.055	5.5	9.3	
	1.060	5.9	9.0	
6:1	1.063	6.2	7.1	
	1.065	6.4	6.3	
	1.070	6.8	5.2	
5:1	1.073	7.1	4.4	
	1.075	7.3	3.7	
	1.080	7.7	2.3	
	1.081	7.8	2.0	
	1.082	7.9	1.7	
	1.083	8.0	1.5	
	1.084	8.1	1.2	
	1.085	8.1	0.9	
	1.086	8.2	0.6	
	1.087	8.3	0.3	
4:1	**1.088**	**8.4**	**0**	**0**
	1.089	8.5		1
	1.090	8.6		2
	1.091	8.7		3
	1.092	8.8		4
	1.093	8.8		5
	1.095	9.0		8
	1.100	9.4		13
	1.105	9.9		19
3:1	1.110	10.3		25
	1.115	10.7		31
	1.120	11.2		36
	1.125	11.6		42
	1.130	12.0		48
	1.135	12.4		54
	1.140	12.8		60
	1.145	13.3		66

(con.)

Table 7.—(Con)

Dilution ratio	Measured specific gravity of the retardant filtrate	Percent by weight P_2O_5	Correction required per 100 gallons of retardant solution: Retardant	Water
			----- Gallons -----	
2:1	1.146	13.3		67
	1.150	13.7		72
	1.155	14.1		77
	1.160	14.5		84
	1.165	14.9		90
	1.170	15.3		96
	1.175	15.7		102
	1.180	16.1		108
	1.185	16.5		114
	1.190	16.9		120
	1.195	17.3		126
	1.200	17.7		132
	1.205	18.1		138
	1.210	18.5		145
1:1	1.214	18.8		150
	1.215	18.9		151
	1.220	19.3		157
	1.225	19.7		163
	1.230	20.0		170
	1.235	20.4		176
	1.240	20.8		182
	1.245	21.1		189
	1.250	21.6		195
	1.275	23.5		228
	1.300	25.3		260
	1.325	27.1		294
	1.350	28.9		328
	1.375	30.6		362
Conc	1.394	31.9		389
	1.400	32.3		397
	1.425	34.0		433
	1.450	35.7		469
	1.475	37.3		505
	1.500	38.9		542

The boxed area represents a variation in salt content such that no corrective action is needed

Table 8.—Salt content of Fire-Trol 931-L related to refractometer scale reading (use with procedure 13)

Dilution ratio	Refractometer scale reading for the retardant	Percent by weight P_2O_5	Correction required per 100 gallons of retardant solution: Retardant	Correction required per 100 gallons of retardant solution: Water
			----- Gallons -----	
20:1	4.1	2.1	19.1	
15:1	5.3	2.8	17.2	
10:1	7.6	4.0	13.6	
9:1	8.3	4.4	12.5	
8:1	9.1	4.9	11.2	
	9.5	5.1	10.5	
	10.0	5.3	9.7	
	10.3	5.5	9.2	
7:1	10.5	5.6	8.9	
	11.0	5.9	8.0	
	11.5	6.2	7.2	
6:1	11.6	6.2	7.0	
	12.0	6.4	6.3	
	12.5	6.7	5.5	
	13.0	7.0	4.6	
5:1	13.2	7.1	4.3	
	13.5	7.3	3.7	
	14.0	7.5	2.9	
	14.5	7.8	2.0	
	15.0	8.1	1.1	
	15.5	8.3	0.2	
4:1	**15.6**	**8.4**	**0**	**0**
	16.0	8.6		3
	16.5	8.9		6
	17.0	9.2		10
	17.5	9.5		14
	18.0	9.7		17
	18.5	10.0		21
	19.0	10.3		25
3:1	19.1	10.3		26
	19.5	10.5		29
	20.0	10.8		32
	20.5	11.1		36
	21.0	11.4		40
	21.5	11.6		44
	22.0	11.9		48
	22.5	12.2		52
	23.0	12.5		56
	23.5	12.7		60
	24.0	13.0		64
	24.5	13.3		68
2:1	24.6	13.3		69
	25.0	13.6		72
	25.5	13.8		76
	26.0	14.1		80
	26.5	14.4		85
	27.0	14.6		89
	27.5	14.9		93
	28.0	15.2		97
	28.5	15.5		102
	29.0	15.7		106
	29.5	16.0		111
	30.0	16.3		115

The boxed area represents a variation in salt content such that no corrective action is needed.

Phos-Chek® 259-W, 259-R, and 259-F.—Phos-Chek 259-W, 259-R, and 259-F are diammonium phosphate-based (DAP) retardants designed for all types of air or ground application. Phos-Chek 259-W is uncolored (W-white), while 259-R contains iron oxide coloring (R-red), and 259-F contains a fugitive coloring agent (F-fugitive). (Fugitive coloring agents fade to a neutral shade several weeks after application.) Phos-Chek 259-W, 259-R, and 259-F contain a low concentration of gum thickener to improve drop characteristics. The products also contain bactericide and corrosion inhibitors. They are the only products relatively noncorrosive to magnesium, thus enhancing their application by helicopter. The three formulations are suitable for ground, helicopter (fixed tank or bucket), or airtanker application at either a mixing rate of 1.14 lb/gal (10.9% DAP) or 1.60 lb/gal (14.5% DAP). Although the higher concentration at high-use level provided greater line-building capability, the limited flexibility of application systems (air or ground) as well as increased cost has generally preclude their use at other than the lower (1.14 lb/gal) use level.

Application	: Ground tanker, fixed-tank helicopter bucket, or airtanker.
Use level	: 1.14 lb of dry retardant mixed with 1 gal of water will produce 1.063 gal of mixed retardant. Each gallon of mixe retardant contains the equivalent of 1.07 lb of powder. 1.60 lb of dry retardant mixed with 1 gal of water will produce 1.094 gal of mixed retardant. Each gallon of mixe retardant contains the equivalent of 1.46 lb of powder in each gallon of slurry.
Viscosity	: 50-150 centipoise (cP).
	: Field measurement (Marsh funnel): 42-62 sec through the small tip (proce dure 8 and table 22 for conversions to viscosity and acceptable range).
Salt content	: 10.9% by weight DAP ($(NH_4)_2HPO_4$) 1.14 lb/gal use level. 14.5% by weight DAP ($(NH_4)_2HPO_4$) 1.60 lb/gal use level.
	: Field measurement (hydrometer): a reading of 1.068 at 80 °F (procedure 3 and table 9) for Phos-Chek 259 mixed at 1.14 lb/gal or 1.089 at 80 °F (proce dure 3 and table 10 for Phos-Chek 259 mixed at 1.60 lb/gal).
Specific weight:	8.90 lb/gal slurry at the 1.14 lb/gal us level and 9.07 lb/gal slurry at the 1.60 lb/gal use level (procedure 9, 10, or 11

T-le 9.—Salt content of Phos-Chek 259-R, 259-F, and 259-W mixed at 1.14 lb/gal related to specific gravity at 80 °F (use with procedure 3)

[illegible]asured specific gravity of the retardant	Percent by weight $(NH_4)_2HPO_4$	Percent by weight P_2O_5 equivalent	Correction required per 100 gallons of retardant solution	
			Retardant	Water
			Lb	*Gal*
1.015	1.6	0.9	98	
1.020	2.5	1.4	89	
1.025	3.4	1.8	81	
1.030	4.3	2.3	71	
1.035	5.1	2.8	62	
1.040	6.0	3.2	53	
1.045	6.9	3.7	44	
1.050	7.7	4.2	35	
1.055	8.6	4.6	25	
1.060	9.5	5.1	16	
1.063	10.0	5.4	10	
1.064	10.2	5.5	8	
1.065	10.3	5.6	6	
1.066	10.5	5.7	4	
1.067	10.7	5.8	2	
1.068	**10.9**	**5.8**	**0**	**0**
1.069	11.1	5.9		2
1.070	11.2	6.0		3
1.071	11.4	6.1		5
1.072	11.6	6.2		7
1.073	11.7	6.3		9
1.074	11.9	6.4		10
1.075	12.1	6.5		12
1.080	13.0	7.0		21
1.085	13.8	7.4		29
1.090	14.7	7.9		38
1.095	15.6	8.4		47
1.100	16.4	8.8		56
1.105	17.3	9.3		65
1.110	18.2	9.8		75
1.115	19.1	10.2		84
1.120	19.9	10.7		93
1.125	20.8	11.2		103
1.130	21.7	11.7		112
1.135	22.5	12.1		122
1.140	23.4	12.6		131
1.145	24.3	13.1		141
1.150	25.2	13.5		151

[illegible]e boxed area represents a variation in salt content such that no corrective action is [illegible]eded.

Table 10.—Salt content of Phos-Chek 259-R, 259-F, and 259-W mixed at 1.60 lb/gal related to specific gravity at 80 °F (use with procedure 3)

Measured specific gravity of the retardant	Percent by weight $(NH_4)_2HPO_4$	Percent by weight P_2O_5 equivalent	Correction required per 100 gallons of retardant solution	
			Retardant	Water
			Lb	*Gal*
1.035	5.1	2.8	107	
1.040	6.0	3.2	98	
1.045	6.9	3.7	88	
1.050	7.7	4.2	79	
1.055	8.6	4.6	69	
1.060	9.5	5.1	59	
1.065	10.3	5.6	49	
1.070	11.2	6.0	39	
1.075	12.1	6.5	29	
1.080	13.0	7.0	19	
1.084	13.7	7.3	11	
1.085	13.8	7.4	9	
1.086	14.0	7.5	7	
1.087	14.2	7.6	5	
1.088	14.4	7.7	3	
1.089	**14.6**	**7.8**	**0**	**0**
1.090	14.7	7.9		1
1.091	14.9	8.0		2
1.092	15.1	8.1		4
1.093	15.2	8.2		5
1.094	15.4	8.3		6
1.095	15.6	8.4		8
1.100	16.4	8.8		14
1.105	17.3	9.3		21
1.110	18.2	9.8		28
1.115	19.1	10.2		34
1.120	19.9	10.7		41
1.125	20.8	11.2		48
1.130	21.7	11.7		55
1.135	22.5	12.1		62
1.140	23.4	12.6		69
1.145	24.3	13.1		76
1.150	25.2	13.5		84
1.155	26.0	14.0		91
1.160	26.9	14.5		98
1.165	26.8	14.9		106
1.170	28.6	15.4		113
1.175	29.5	15.9		120

The boxed area represents a variation in salt content such that no corrective action is needed

Gum-Thickened Retardants

Phos-Chek® A-W, A-R, and A-F.—Phos-Chek A-W, A-R, and A-F are gum-thickened monoammonium phosphate-based retardant formulations approved for airtanker application. Phos-Chek A-W is uncolored (W-white) while A-R contains iron oxide coloring (R-red) and A-F contains a fugitive coloring agent (F-fugitive). (Fugitive coloring agents fade to a neutral shade several weeks after application.) Because they contain a relatively high concentration of gum-thickener to provide a high viscosity (approximately 1,500 centipoise) for improved drop characteristics from fixed-wing airtankers, these formulations are not recommended for ground or helicopter use. The products also contain viscosity stabilizers and corrosion inhibitors.

Application : Airtanker.

Use level : 0.96 lb of dry retardant mixed with 1 gal of water will produce 1.057 gal of mixed retardant. Each gallon of mixe retardant contains the equivalent of 0.908 lb of powder.

Viscosity : 1,200-1,800 centipoise (cP).

: Field measurement (Marsh funnel): 28-38 sec through the large tip (proce dure 8 and table 22 show conversion to viscosity and acceptable range).

Salt content : 9.0% by weight MAP ($NH_4H_2PO_4$).

: Field measurement (hydrometer): a reading of 1.057 at 80 °F (procedure and table 11 for conversion to salt co tent and acceptable range).

: Field measurement (refractometer): a reading of 7.9 (procedure 13 and table 12 for conversion to salt content and acceptable range).

Specific weight: 8.78 lb/gal slurry (procedure 9, 10, or 1

Table 11.—Salt content of Phos-Chek A-R, A-F, and A-W related to specific gravity at 80 °F (use with procedure 4)

Measured specific gravity of the thinned retardant	Percent by weight $NH_4H_2PO_4$	Percent by weight P_2O_5 equivalent	Correction required per 100 gallons of retardant solution: Retardant	Water
			Lb	*Gal*
1.025	3.6	2.2	59	
1.030	4.5	2.8	50	
1.035	5.3	3.3	41	
1.040	6.2	3.8	31	
1.045	7.0	4.3	22	
1.050	7.9	4.9	13	
1.051	8.1	5.0	11	
1.052	8.2	5.1	9	
1.053	8.4	5.2	7	
1.054	8.6	5.3	5	
1.055	8.7	5.4	3	
1.056	8.9	5.5	1	
1.057	**9.0**	**5.6**	**0**	**0**
1.058	9.2	5.7		3
1.059	9.4	5.8		5
1.060	9.6	5.9		7
1.061	9.7	6.0		9
1.062	9.9	6.1		11
1.065	10.4	6.4		17
1.070	11.3	7.0		27
1.075	12.1	7.5		37
1.080	13.0	8.0		48
1.085	13.8	8.5		58
1.090	14.7	9.1		69
1.095	15.5	9.6		79
1.100	16.4	10.1		90
1.105	17.2	10.6		101
1.110	18.1	11.2		112
1.115	18.9	11.7		123
1.120	19.8	12.2		134
1.125	20.6	12.7		145

The boxed area represents a variation in salt content such that no corrective action is needed.

Table 12.—Salt content of Phos-Chek A-R, A-F, and A-W related to refractom scale reading (use with procedure 4)

Refractometer scale reading for the retardant	Percent by weight $NH_4H_2PO_4$	Percent by weight P_2O_5 equivalent	Correction required per 100 gallons of retardant soluti: Retardant	W[illegible]
			Lb	[illegible]
3.5	3.7	2.3	57	
4.0	4.3	2.7	51	
4.5	4.9	3.0	45	
5.0	5.5	3.4	39	
5.5	6.0	3.7	33	
6.0	6.6	4.1	26	
6.5	7.2	4.5	20	
7.0	7.9	4.8	13	
7.5	8.5	5.2	6	
7.9	**9.0**	**5.6**	**0**	[illegible]
8.0	9.1	5.6		[illegible]
8.5	9.7	6.0		[illegible]
9.0	10.4	6.4		[illegible]
9.5	11.1	6.8		[illegible]
10.0	11.7	7.2		[illegible]
10.5	12.4	7.7		[illegible]
11.0	13.1	8.1		[illegible]
11.5	13.8	8.5		[illegible]
12.0	14.5	9.0		[illegible]
12.5	15.2	9.4		[illegible]
13.0	16.0	9.8		[illegible]
13.5	16.7	10.3		[illegible]
14.0	17.5	10.8		[illegible]
14.5	18.2	11.2		[illegible]
15.0	19.0	11.7		[illegible]
15.5	19.8	12.2		[illegible]
16.0	20.6	12.7		[illegible]
16.5	21.4	13.2		[illegible]
17.0	22.3	13.7		[illegible]
17.5	23.1	14.3		[illegible]

The boxed area represents a variation in salt content such that no corrective action is needed.

Phos-Chek® D75-R and D75-F.—Phos-Chek D75-R and 75-F are formulations comprised of a mixture of onoammonium phosphate and ammonium sulfate as e active fire retardant salts. The formulations are proved for airtanker application. Due to their high scosity, they are not recommended for application by ound tanker or helicopter. D75-R contains iron oxide loring (R-red) and D75-F contains a fugitive coloring gent (F-fugitive). (Fugitive coloring agents fade to a utral shade several weeks after application.) Both formulations contain a relatively high concentration of gum ickener to provide a high viscosity (approximately 500 centipoise) for improved drop characteristics from rtankers. The products also contain viscosity abilizers and corrosion inhibitors.

Application	:	Airtanker.
Jse level	:	1.20 lb of dry retardant mixed with 1 gal of water will produce 1.069 gal of mixed retardant. Each gallon of mixed retardant contains the equivalent of 1.12 lb of powder.

ble 13.—Salt content of Phos-Chek D75-R and D75-F related to specific gravity at 80 °F (use with procedure 4)

easured specific gravity of the inned retardant	Percent by weight active salt $(NH_4)_2SO_4/NH_4H_2PO_4$	Correction required per 100 gallons of retardant solution: Retardant	Water
		Lb	*Gal*
1.020	3.2	87.9	
1.025	4.0	79.5	
1.030	4.8	71.1	
1.035	5.6	62.6	
1.040	6.4	54.0	
1.045	7.2	45.5	
1.050	8.0	36.9	
1.055	8.8	28.2	
1.060	9.6	19.6	
1.065	10.3	10.8	
1.066	10.5	9.1	
1.067	10.6	7.3	
1.068	10.8	5.6	
1.069	11.0	3.8	
1.070	11.1	2.1	
1.071	**11.3**	**0**	**0**
1.072	11.4		1
1.073	11.6		3
1.074	11.7		4
1.075	11.9		6
1.076	12.0		7
1.077	12.2		9
1.078	12.3		10
1.080	12.6		13
1.085	13.4		20
1.090	14.2		28
1.095	14.9		35
1.100	15.7		43
1.105	16.4		50
1.110	17.2		58
1.115	17.9		65
1.120	18.6		73
1.125	19.4		81

e boxed area represents a variation in salt content such that no correce action is needed.

Viscosity	:	1,200-1,800 centipoise (cP).
	:	Field measurement (Marsh funnel): 28-56 sec through the large tip (procedure 8 and table 22 show conversion to viscosity and acceptable range).
Salt content	:	11.20% by weight active salt: 8.43% by weight AS ($(NH_4)_2SO_4$) and 2.77% MAP ($NH_4H_2PO_4$).
	:	Field measurement (hydrometer): a reading of 1.071 at 80 °F (procedure 4 and table 13 for conversion to salt content and acceptable range).
	:	Field measurement (refractometer): a reading of 12.1 (procedure 13 and table 14 for conversion to salt content and acceptable range).
Specific weight:		8.91 lb/gal slurry (procedure 9, 10, or 11).

Table 14.—Salt content of Phos-Chek D75-R and D75-F related to refractometer scale reading (use with procedure 13)

Refractometer scale reading for the retardant	Percent by weight active salt $(NH_4)_2SO_4/NH_4H_2PO_4$	Correction required per 100 gallons of retardant solution: Retardant	Water
		Lb	*Gal*
3.5	3.2	88.4	
4.0	3.6	83.5	
4.5	4.1	78.6	
5.0	4.6	73.6	
5.5	5.1	68.7	
6.0	5.5	63.7	
6.5	6.0	58.6	
7.0	6.5	53.6	
7.5	6.9	48.5	
8.0	7.4	43.4	
8.5	7.9	38.2	
9.0	8.3	33.1	
9.5	8.8	27.9	
10.0	9.3	22.6	
10.5	9.8	17.4	
11.0	10.2	12.1	
11.5	10.7	6.7	
12.0	11.2	1.4	
12.1	**11.3**	**0**	**0**
12.5	11.6		3
13.0	12.1		8
13.5	12.6		12
14.0	13.0		17
14.5	13.5		21
15.0	14.0		26
15.5	14.5		31
16.0	14.9		35
16.5	15.4		40
17.0	15.9		45
17.5	16.3		49
18.0	16.8		54
18.5	17.3		59
19.0	17.7		64
19.5	18.2		69
20.0	18.7		73

The boxed area represents a variation in salt content such that no corrective action is needed.

Fire-Trol® GTS-R and GTS-F.—Fire-Trol GTS-R and GTS-F formulations contain ammonium sulfate as the primary active fire retardant salt. They also contain a small amount of ammonium phosphate that acts as both a corrosion inhibitor and a retardant salt. The formulations are designed for airtanker application; Fire-Trol GTS-R is iron oxide colored (R-red) while GTS-F contains a fugitive coloring agent (F-fugitive). (Fugitive coloring agents fade to a neutral shade several weeks after application.) Both formulations contain a relatively high concentration of gum thickener to provide a high viscosity (approximately 1,500 centipoise) for improved drop characteristics from airtankers. Due to the high viscosity these formulations are not normally used for ground or helicopter use. The products also contain spoilage and additional corrosion inhibitors.

Application	: Airtanker.
Use level	: 1.76 lb of dry retardant mixed with 1 gal of water will produce 1.10 gal of mixed retardant. Each gallon of mixed retardant contains the equivalent of 1.59 lb of powder.
Viscosity	: 1,200-1,800 centipoise (cP).
	: Field measurement (Marsh funnel): 36-52 sec through the large tip (proce dure 8 and table 22 for conversions t viscosity and acceptable range).
Salt content	: 14.81% by weight AS ($(NH_4)_2SO_4$) an 1.26% DAP ($(NH_4)_2HPO_4$).
	: Field measurement (hydrometer): a reading of 1.098 at 80 °F (procedure and table 15 for conversion to salt co tent and acceptable range).
	: Field measurement (refractometer): a reading of 16.4 on the unthinned retardant, (procedure 13 and table 16 for conversion to salt content and acceptable range).
Specific weight:	9.13 lb/gal slurry (procedure 9, 10, or

Table 15.—Salt content of Fire-Trol GTS-R and GTS-F related to specific gravity at 80 °F (use with procedure 4)

Measured specific gravity of the thinned retardant	Percent by weight $(NH_4)_2SO_4$	Correction required per 100 gallons of retardant solution: Retardant	Water
		Lb	*Gal*
1.050	5.9	111	
1.055	6.8	100	
1.060	7.8	89	
1.065	8.7	78	
1.070	9.6	66	
1.075	10.5	55	
1.080	11.5	43	
1.085	12.4	31	
1.090	13.3	19	
1.091	13.5	17	
1.092	13.7	15	
1.093	13.9	12	
1.094	14.1	10	
1.095	14.3	7	
1.096	14.4	5	
1.097	14.6	3	
1.098	**14.8**	**0**	**0**
1.099	15.0		1
1.100	15.2		3
1.101	15.4		4
1.102	15.5		5
1.103	15.7		7
1.104	15.9		8
1.105	16.1		10
1.106	16.3		11
1.110	17.0		17
1.115	17.9		24
1.120	18.9		31
1.125	19.8		38
1.130	20.7		45
1.135	21.7		52
1.140	22.6		60
1.145	23.5		67
1.150	24.4		75

The boxed area represents a variation in salt content such that no corrective action is needed

Table 16.—Salt content of Fire-Trol GTS-R and GTS-F related to refractometer scale reading at 80 °F (use with procedure 13)

Refractometer scale reading for the retardant	Percent by weight active salt $(NH_4)_2SO_4$	Correction required per 100 gallons of retardant solution: Retardant	Water
		Lb	*Gal*
7.0	5.9	111	
7.5	6.4	105	
8.0	6.9	99	
8.5	7.4	94	
9.0	7.8	88	
9.5	8.3	82	
10.0	8.8	77	
10.5	9.2	71	
11.0	9.7	65	
11.5	10.2	59	
12.0	10.6	53	
12.5	11.1	47	
13.0	11.6	42	
13.5	12.0	36	
14.0	12.5	30	
14.5	13.0	24	
15.0	13.5	18	
15.5	13.9	12	
16.0	14.4	6	
16.4	**14.8**	**0**	**0**
16.5	14.9		1
17.0	15.3		4
17.5	15.8		7
18.0	16.3		11
18.5	16.7		14
19.0	17.2		18
19.5	17.7		21
20.0	18.1		25
20.5	18.6		29
21.0	19.1		32
21.5	19.5		36
22.0	20.0		40
22.5	20.5		43
23.0	21.0		47
23.5	21.4		51
24.0	21.9		54
24.5	22.4		58
25.0	22.8		62
25.5	23.3		66
26.0	23.8		69
26.5	24.2		73
27.0	24.7		77
27.5	25.2		81

The boxed area represents a variation in salt content such that no corrective action is needed.

Phos-Chek® XB.—Phos-Chek XB is a monoammonium phosphate-based product containing a gum thickener. It is produced and sold for use in Canada and some overseas markets. Minor ingredients include corrosion inhibitors, viscosity stabilizers, and coloring agents.

Application	: Airtanker.
Use level	: 1.14 lb of dry retardant mixed with 1 gal (U.S.) of water will produce 1.074 gal of mixed retardant. Each gallon of mixed retardant contains the equivalent of 1.06 lb of dry retardant.
Viscosity	: 1,200-1,800 centipoise (cP).
	: Field measurement (Marsh funnel): 34-50 sec through the large tip (procedure 8 and table 22 for conversions to viscosity and acceptable range).
Salt content	: 10.65% by weight MAP ($NH_4H_2PO_4$).
	: Field measurement (hydrometer): a reading of 1.056 at 80 °F (procedure 4 and table 17 for conversion to salt content and acceptable range).
Specific weight:	8.81 lb/gal slurry (procedure 9, 10, or 11).

Table 17.—Salt content of Phos-Chek XB related to specific gravity at 80 °F (use with procedure 4)

Measured specific gravity of the thinned retardant	Percent by weight $NH_4H_2HPO_4$	Percent by weight P_2O_5 equivalent	Correction required per 100 gallons of retardant solution	
			Retardant	Water
			Lb	*Gal*
1.015	3.5	2.2	77	
1.020	4.4	2.7	68	
1.025	5.3	3.2	59	
1.030	6.1	3.8	50	
1.035	7.0	4.3	41	
1.040	7.8	4.8	31	
1.045	8.7	5.4	22	
1.050	9.6	5.9	12	
1.052	9.9	6.1	8	
1.053	10.1	6.2	6	
1.054	10.3	6.3	5	
1.055	10.5	6.4	3	
1.056	**10.7**	**6.6**	**0**	**0**
1.057	10.8	6.7		1
1.058	10.9	6.8		3
1.059	11.1	6.9		5
1.060	11.3	7.0		6
1.061	11.5	7.1		8
1.065	12.1	7.5		15
1.070	13.0	8.0		24
1.075	13.9	8.6		32
1.080	14.7	9.1		41
1.085	15.6	9.6		50
1.090	16.4	10.2		59
1.095	17.3	10.7		68
1.100	18.2	11.2		78
1.105	19.0	11.7		87
1.110	19.9	12.3		96
1.115	20.7	12.8		106
1.120	21.6	13.3		115
1.125	22.5	13.9		125
1.130	23.3	14.4		135
1.135	24.2	14.9		144
1.140	25.0	15.5		154

The boxed area represents a variation in salt content such that no corrective action is needed.

Megatard® 2700-R and 2700-F.—Megatard 2700-R and 2700-F are two-component systems. One component contains a water solution of ammonium sulfate and corrosion inhibitor, liquified at the time of delivery at the base. The other component contains a gum thickener, coloring agent, and spoilage inhibitor. Megatard 2700 is colored with either iron-oxide (R-red) or a fugitive coloring (F-fugitive). (Fugitive coloring agents fade to a neutral shade several weeks after application.) The two components are pumped together with additional water to produce the mixed retardant with a relatively high viscosity suitable for fixed-wing air application. Megatard 2700 is designed to be pumped directly into an aircraft as the final product is not storable.

Application	:	Airtanker.
Use level	:	1.00 gal liquified ammonium sulfate (LS) + 0.244 lb of thickener/color package added to 1.00 gal of water will produce 2.01 gal of mixed retardant. Each gallon of mixed retardant contains the equivalent of 0.50 gal of LS and 0.116 lb of thickener/color package.
Viscosity	:	Mixed retardant: 1,200-1,800 centipoise (cP).
	:	Field measurement (Marsh funnel) of mixed retardant: 30-44 sec through the large tip (procedure 8 and table 22 for conversions to viscosity and acceptable range).
Salt content	:	28.2% and 15.0% by weight AS ($(NH_4)_2SO_4$), respectively, of liquified sulfate and mixed retardant.
	:	Field measurement (hydrometer): Liquified sulfate: a reading of 1.166 at 80 °F (procedure 3 and table 18 for conversion to salt content and acceptable range). Mixed retardant: a reading of 1.096 at 80 °F (procedure 4 and table 19 for conversion to salt content and acceptable range).
Specific weight	:	9.71 and 9.07 lb/gal slurry, respectively, for liquified sulfate and mixed retardant (procedure 9, 10, or 11).

Table 18.—Salt content of Megatard 2700 liquified sulfate related to specific gravity at 80 °F (use with procedure 3)

Measured specific gravity of the retardant	Percent by weight $(NH_4)_2SO_4$	Correction required per 100 gallons of retardant solution: Retardant	Correction required per 100 gallons of retardant solution: Water
		Lb	*Gal*
1.100	16.5	164	
1.105	17.4	152	
1.110	18.3	140	
1.115	19.2	129	
1.120	20.0	117	
1.125	20.9	104	
1.130	21.8	92	
1.135	22.7	80	
1.140	23.6	67	
1.145	24.5	55	
1.150	25.3	42	
1.155	26.2	29	
1.159	26.9	19	
1.160	27.1	16	
1.161	27.3	13	
1.162	27.4	11	
1.163	27.6	8	
1.164	27.8	6	
1.165	28.0	3	
1.166	**28.2**	**0**	**0**
1.167	28.3		1
1.168	28.5		1
1.169	28.7		2
1.170	28.9		3
1.171	29.0		4
1.172	29.2		4
1.173	29.4		5
1.174	29.6		6
1.175	29.7		7
1.180	30.6		10
1.185	31.5		14
1.190	32.4		18
1.195	33.3		22
1.200	34.1		25
1.205	35.0		29
1.210	35.9		33
1.215	36.8		37
1.220	37.7		41
1.225	38.6		45
1.230	39.4		49
1.235	40.2		53

The boxed area represents a variation in salt content such that no corrective action is needed.

Table 19.—Salt content of Megatard 2700 related to specific gravity at 80 °F (use with procedure 4)

Measured specific gravity of the thinned retardant	Percent by weight $(NH_4)_2SO_4$	Correction required per 100 gallons of retardant solution	
		Retardant	Water
		Lb	*Gal*
1.025	3.8	75	
1.030	4.5	70	
1.035	5.3	65	
1.040	6.1	60	
1.045	6.9	55	
1.050	7.7	50	
1.055	8.5	45	
1.060	9.3	39	
1.065	10.1	34	
1.070	10.8	29	
1.075	11.6	23	
1.080	12.4	18	
1.085	13.2	13	
1.087	13.5	10	
1.088	13.7	9	
1.089	13.8	8	
1.090	14.0	7	
1.091	14.1	6	
1.092	14.3	5	
1.093	14.5	4	
1.094	14.6	3	
1.095	14.8	2	
1.096	**15.0**	**0**	**0**
1.097	15.1		1
1.098	15.2		2
1.099	15.4		3
1.100	15.6		4
1.101	15.7		5
1.102	15.9		7
1.103	16.0		8
1.104	16.2		9
1.105	16.3		10
1.106	16.5		11
1.110	17.1		16
1.115	17.9		22
1.120	18.7		28
1.125	19.5		34
1.130	20.3		40
1.135	21.1		46
1.140	21.9		52
1.145	22.6		59
1.150	23.4		65

The boxed area represents a variation in salt content such that no corrective action is needed.

Clay-Thickened Retardants

Fire-Trol® 100.—Fire-Trol 100 uses ammonium sulfate as its active retardant salt. It is a clay-thickened product designed for airtanker application. Its viscosity is developed by shearing (or separating) the clay during the mixing process, usually in 500- or 1,000-gal batch mixers. Iron oxide is used as a coloring agent. A corrosion inhibitor is added to protect the aircraft and mixing and storage equipment.

Application	: Airtanker.
Use level	: 2.78 lb of dry retardant added to 1 gal of water will produce 1.182 gal of mixed retardant. Each gallon of mixed retardant contains the equivalent of 2.35 lb of dry retardant.
Viscosity	: 1,500-2,500 centipoise (cP).
	: Field measurement (Marsh funnel): 20-40 sec through the large tip (procedure 8 and table 22 for conversions to viscosity and acceptable range).
Salt content	: 15.6% by weight AS ($(NH_4)_2SO_4$).
	: Field measurement (hydrometer): a reading of 1.100 at 80 °F (procedure 5 and table 20 for conversion to salt content and acceptable range).
	: Field measurement (refractometer): a reading of 17.2 (procedure 13 and table 21 for conversion to salt content and acceptable range).
Specific weight:	9.40 lb/gal slurry (procedure 9, 10, or 11).

Table 20.—Salt content of Fire-Trol 100 related to specific gravity at 80 °F (use with procedure 5)

Measured specific gravity of the retardant filtrate	Percent by weight $(NH_4)_2SO_4$	Correction required per 100 gallons of retardant solution	
		Retardant	Water
		Lb	*Gal*
1.025	4.2	208	
1.030	5.0	194	
1.035	5.8	180	
1.040	6.6	167	
1.045	7.4	153	
1.050	8.2	139	
1.055	9.0	125	
1.060	9.7	111	
1.065	10.5	97	
1.070	11.2	83	
1.075	12.0	70	
1.080	12.7	56	
1.085	13.4	42	
1.090	14.2	28	
1.091	14.3	25	
1.092	14.5	23	
1.093	14.6	20	
1.094	14.7	17	
1.095	14.9	14	
1.096	15.0	12	
1.097	15.2	9	
1.098	15.3	6	
1.099	15.5	3	
1.100	**15.6**	**0**	**0**
1.101	15.7		1
1.102	15.9		2
1.103	16.0		3
1.104	16.2		4
1.105	16.3		5
1.106	16.4		6
1.107	16.6		7
1.108	16.7		8
1.109	16.9		9
1.110	17.0		10
1.111	17.1		11
1.115	17.7		15
1.120	18.4		20
1.125	19.1		25
1.130	19.7		30
1.135	20.4		35
1.140	21.1		40
1.145	21.7		45
1.150	22.4		50
1.155	23.0		55
1.160	23.6		60
1.165	24.3		65
1.170	24.9		70
1.175	25.5		75

The boxed area represents a variation in salt content such that no corrective action is needed.

Table 21.—Salt content of Fire-Trol 100 related to refractometer scale reading at 80 °F (use with procedure 13)

Refractometer scale reading for the retardant	Percent by weight $(NH_4)_2SO_4$	Correction required per 100 gallons of retardant solution	
		Retardant	Water
		Lb	*Gal*
7.0	6.4	171	
7.5	6.8	163	
8.0	7.3	155	
8.5	7.7	147	
9.0	8.2	139	
9.5	8.6	131	
10.0	9.1	123	
10.5	9.6	114	
11.0	10.0	106	
11.5	10.5	98	
12.0	10.9	89	
12.5	11.4	81	
13.0	11.8	72	
13.5	12.3	64	
14.0	12.7	55	
14.5	13.2	47	
15.0	13.6	38	
15.5	14.1	29	
16.0	14.6	21	
16.5	15.0	12	
17.0	15.5	3	
17.2	**15.6**	**0**	**0**
17.5	15.9		2
18.0	16.4		5
18.5	16.8		9
19.0	17.3		12
19.5	17.7		15
20.0	18.2		18
20.5	18.6		22
21.0	19.1		25
21.5	19.6		28
22.0	20.0		32
22.5	20.5		35
23.0	20.9		39
23.5	21.4		42
24.0	21.8		46
24.5	22.3		49
25.0	22.7		53

The boxed area represents a variation in salt content such that no corrective action is needed.

SHORT-TERM RETARDANT FORMULATIONS

Fire-Trol® ST-Poly.—Fire-Trol ST-Poly (formerly referred to as Poly-Trol) is a formulation developed for thickening water to improve its drop characteristics for fixed-wing aerial application. Fire-Trol ST-Poly contains both a coloring agent and corrosion inhibitor, but is primarily a synthetic acrylamide polymer which requires a low use level to achieve acceptable viscosity and/or elasticity.

Application	: Airtanker or helicopter bucket.
Use level	: 0.50% to 0.7% by weight. Use levels are dependent on water temperature and water hardness. An appropriate use level within the above range should be established using procedure 8 and table 22 as a guide. Changes in water source or quality (hardness) may necessitate a change in the appropriate use level. In general, use levels in the 0.50 to 0.75 range will provide drop performance similar to a "gum-thickened" retardant.
Viscosity	: 150-250 centipoise (cP).
	: Field measurement (Marsh funnel): 54-72 sec through the small tip (procedure 8 and table 22 show conversions to viscosity and acceptable range).
Specific weight:	8.34 lb/gal slurry (procedure 9, 10, or 11).

Fire-Kill® IIP.—Fire-Kill IIP is a short-term retardant formulation composed of xanthan gum and synthetic polymer thickener. Fire-Kill IIP also contains corrosion and spoilage inhibitors and coloring. The thickeners function to improve drop characteristics for airtanker or helicopter application.

Application	: Airtanker or helicopter bucket.
Use level	: 0.25% by weight for helicopter application; 0.50% to 0.7% by weight for fixed-wing airtanker.. Use levels are dependent on water temperature and water hardness. An appropriate use level within the above ranges should be established using procedure 8 and table 22 as a guide. Changes in water source or quality (hardness) may necessitate a change in the appropriate use level. In general, use levels in the 0.50 to 0.75 range will provide drop performance similar to a "gum-thickened" retardant.
Viscosity	: 150-250 centipoise (cP).
	: Field measurement (Marsh funnel): 46-54 sec through the small tip (procedure 8 and table 22 show conversions to viscosity and acceptable range).
Specific weight:	8.34 lb/gal slurry (procedure 9, 10, or 11).

PROCEDURES

Procedure 1: Sampling a Storable Retardant for Testing

Guidelines are given for obtaining a representative sample of the material in storage for quality control testing.

1. Recirculate the retardant in the tanks after a major mixing operation, then take a sample from a recirculation line or pump.
2. Recirculate tanks and take a sample at least every 7 days during periods when there is little activity.
3. During mixing operations, take samples often enough to ensure that the mixed product meets the requirements for the specific retardant.
4. Use fresh samples from sampling valve or line after product has been pumped or circulated. Do not use slurry that has been sitting in hoses, pumps, or valves.
5. If a sample is taken from the end of the hose, be sure that sufficient retardant has been pumped through the hose to ensure a fresh sample.
6. If significant deterioration of stored material is discovered, (a) take a sample of bad material and hold for instructions and/or additional testing, (b) notify appropriate agency personnel of the problem, and (c) notify the supplier of the material.

Procedure 2: Sampling a Nonstorable Retardant for Testing

Guidelines are given for obtaining representative samples of nonstorable retardants for quality control testing.

1. Take samples after enough retardant has been pumped to ensure complete removal of old slurry from hose (immediately after loading an airtanker).
2. Take samples often enough during mixing operations to ensure that the mixed product meets the requirements for the specific retardant.
3. If significant deterioration is discovered in stored concentrate or in mixed retardant stored in aircraft for long periods of time, (a) take a sample of bad material and hold for instructions and/or additional testing, (b) notify appropriate agency personnel of the problem, and (c) notify the supplier of the material.

Procedure 3: Field Determination of Salt Content of Unthickened or Low-Viscosity Gum-Thickened Retardants

(Phos-Chek G-WX, Fire-Trol 934-L, Fire-Trol 936-L, Phos-Chek G-W, G-R, G-F, Fire-Trol 931-L, Phos-Chek 259-W, 259-R, and 259-F, and the liquid sulfate used in producing Megatard 2700)

The salt content of unthickened or low-viscosity retardant can be determined by measuring the specific gravity of an untreated retardant sample with a hydrometer and using tables provided to convert specific gravity to percentage of salt.

1.a. Take a freshly agitated sample of the retardant solution to be analyzed. If possible, allow the sample to reach room temperature (approximately 80 °F).

1.b. For greater accuracy FT 931-L may be filtered prior to determination of the specific gravity (see procedure 5). A separate calibration table (table 7) is provided for use with a filtered solution.

2. After all entrapped air bubbles are allowed to escape, measure the specific gravity of the solution with a hydrometer readable to 0.001 divisions. Let the hydrometer settle in the solution for 3 to 5 min before reading.

3. Read and record the temperature of the retardant to the nearest °F.

4. Record the specific gravity to the nearest 0.001.

5. Using table 26 of appendix 3 or the following rule for deviation of temperature, adjust the specific gravity reading: for every 5 °F the retardant solution temperature is below 80 °F, subtract 0.001 from the hydrometer reading; or for every 5 °F the retardant solution is above 80 °F, add 0.001 to the hydrometer reading.

6. Using the appropriate table (for the retardant being tested), determine the percentage by weight of salt in the solution. The tables also show how to correct retardants with salt content outside acceptable levels.

Procedure 4: Field Determination of Salt Content of High-Viscosity Gum-Thickened Retardants

(Phos-Chek A-W, A-R, and A-F, Phos-Chek D75-R and D75-F, Fire-Trol GTS-R and GTS-F, Phos-Chek XB, and Megatard 2700-R and 2700-F)

A viscosity-reducing agent is used to lower the viscosity of gum-thickened retardants to obtain an accurate specific gravity of the solution using a hydrometer. Retardant salt content can be read directly from the conversion tables provided.

1. Take a freshly agitated sample of the mixed retardant to be analyzed. Allow the sample to reach room temperature (approximately 80 °F).

2. Fill a quart jar one-half full with the retardant sample. Add 2 level teaspoons (using a measuring-type teaspoon) of the appropriate viscosity-reducing agent to the sample.

3. Shake sample and viscosity-reducing agent together vigorously for at least 30 sec, then loosen the lid to relieve gas pressure and allow entrapped air bubbles to escape.

4. Allow the sample to sit for 10 min.

5. Pour the thinned sample into an 8-inch test tube, ease the hydrometer into the sample, and allow it to sit for an additional 10 min.

6. Read and record the temperature of the retardant to the nearest °F.

7. Measure and record the specific gravity of the solution with a hydrometer readable to 0.001 divisions.

8. Using table 26 (appendix 3) or using the following rule for deviation of temperature, adjust the specific gravity reading: for every 5 °F the retardant solution temperature is below 80 °F, subtract 0.001 from the hydrometer reading; or for every 5 °F the retardant solution is above 80 °F, add 0.001 to the hydrometer reading.

9. Use the appropriate tables to determine the percentage by weight of salt in the solution. The tables also show how to correct retardants with salt contents outside acceptable levels.

NOTE: DO NOT ALLOW ANY SOLUTION CONTAINING VISCOSITY-REDUCING AGENT TO BE RETURNED TO THE STORAGE TANK, SINCE A SMALL AMOUNT CAN CAUSE REDUCTION OF VISCOSITY OF THE CONTENTS OF THE ENTIRE TANK.

Procedure 5: Field Determination of Salt Content of Clay-Thickened Retardants

(Fire-Trol 100)

Clay-thickened fire retardants must be filtered to remove the solid particles to obtain an accurate specific gravity. The retardant salt content can be read directly from the conversion tables provided once the specific gravity has been measured with a hydrometer.

1. Take a freshly agitated sample (1 to 1.5 quarts) of the retardant solution to be analyzed.

2. Place the sample in an 8-inch funnel containing a rapid and fairly retentive filter paper. Collect sufficient filtrate to fill an 8-inch test tube (80-100 mL). This will take about 30 min depending partially on the viscosity.

3. Allow the filtrate to reach room temperature (approximately 80 °F) if possible. Read and record the temperature of the filtrate.

4. Allow the hydrometer to settle in the solution for 3 to 5 min.

5. Measure and record the specific gravity to the nearest 0.001.

6. Using table 26 (appendix 3) or the following rule for deviation of temperature, adjust the specific gravity reading: for every 5 °F the retardant solution temperature is below 80 °F, subtract 0.001 from the hydrometer reading; or for every 5 °F the retardant solution is above 80 °F, add 0.001 to the hydrometer reading.

7. Using the appropriate table, determine the percentage by weight of salt in the solution. The tables also show how to correct retardants with salt contents outside the acceptable levels.

Procedure 6: Field Determination of Salt Content of Clay-Thickened Liquid Concentrates

(Fire-Trol 931-L concentrate)

Clay-thickened liquid concentrates must be diluted quantitatively and filtered prior to measuring the specific gravity. Directions are given for making a suitable dilution container and performing the dilution and filtration steps. After the specific gravity has been determined with a hydrometer, the salt content can be read directly from the conversion tables provided.

1. Calibrate a 1-quart container (such as a disposable canteen) with a tight-fitting screw cap:

a. Pour exactly 1 cup (8 fluid oz) of water into the 1-quart container.

b. Accurately mark the water level.
c. Pour another cup of water into the container.
d. Mark the 2-cup level.
e. Empty all water from the container and allow to dry.
f. Repeat steps a through e at least two more times.
g. Mark the final 1- and 2-cup levels with a narrow-tip waterproof marker.

2. Pour a well-mixed sample of Fire-Trol 931 concentrate into the calibrated container, exactly to the 1-cup mark.
3. Add water to the 2-cup mark.
4. Shake thoroughly.
5. Place the sample in an 8-inch funnel containing a rapid and fairly retentive filter paper. Collect sufficient filtrate to fill an 8-inch test tube (80-100 mL). This will take about 30 min, depending partially on the viscosity.
6. Allow the filtrate to reach room temperature (approximately 80 °F) if possible. Read and record the temperature of the filtrate.
7. Allow the hydrometer to settle in the solution for 3 to 5 min.
8. Measure and record the specific gravity to the nearest 0.001.
9. Using table 26 (appendix 3) or the following rule for deviation of temperature, adjust the specific gravity reading: for every 5 °F the retardant solution temperature is below 80 °F, subtract 0.001 from the hydrometer reading; or for every 5 °F the retardant solution is above 80 °F, add 0.001 to the hydrometer reading.
10. Using the appropriate table, determine the percentage by weight of salt in the solution. The tables also show how to correct retardants with salt contents outside the acceptable levels.

Procedure 7: Determining Viscosity Using a Brookfield Viscometer

The viscosity of a retardant can be determined using a calibrated Brookfield viscometer (Model LVF). The standard spindles provided with a Brookfield viscometer moving at a known, constant rate for a defined time period provide the shear while the scale reading multiplied by a constant (specific to the spindle used) gives the viscosity.

1. Level viscometer by adjusting the tripod feet until bubble level is centered. Tighten clamp to hold in this position.
2. Adjust speed control to 60 r/min. (The 60 should be on the upper surface of the knob.)
3. Attach the guard by the screw on each side of the housing.
4. Attach the correct spindle (number 2 for viscosities less than 500 centipoise; number 4 for viscosities greater than 500 centipoise) by screwing it onto the threaded shaft.

NOTE: THIS IS A LEFT-HAND THREAD. Tighten finger-tight only, holding the shaft to prevent movement of the pointer.

5. Immerse the spindle in the liquid to be tested just to the immersion ring on the spindle.
6. Depress clutch. This procedure relieves wear and tear on the "innards" when measuring thick liquids.
7. Turn motor on, release clutch, and allow to rotate for 1 min.
8. Depress clutch to maintain pointer position and turn motor off. If pointer is not in view, turn motor on and off to bring it into view with clutch still depressed.
9. Read dial at pointer position. Clutch can now be released.
10. Calculate viscosity in centipoise by multiplying dial reading by proper factor (5 for spindle 2; 100 for spindle 4).
11. Repeat three times and report average viscosity.

Procedure 8: Determining Slurry Viscosity Using a Marsh Funnel

The time that it takes for a known volume of solution to flow through an orifice of fixed dimension is related to viscosity. Correlation tables have been provided to read viscosity directly from flow-through time.

1. Be sure the proper tip (0.269 ± 0.002-inch diameter for large tip and 0.187 ± 0.002-inch diameter for small tip) is in the Marsh funnel.
2. Use fresh samples that have completely hydrated (approximately one-half to 1 hour after mixing) without excessive air bubbles.
3. Close the funnel tip with a finger and pour retardant **through** the screen into a clean, dry, upright funnel until the fluid level **exactly** reaches the bottom of the screen.
4. Measure the time in minutes and seconds for exactly 1 quart (946 mL) of retardant to flow through the funnel.
5. Look up measured time in left column of table 22. Read the appropriate column for the retardant being tested.

NOTE:

1. The amount of time elapsed since agitation and the retardant temperature influence viscosity. The viscosity values in the table will apply only to retardant at the time and temperature at which the sample is tested.
2. The values in the table are for samples at 75 to 85 °F. Higher temperatures may give falsely low viscosities; lower temperatures may give falsely high viscosities.
3. Numbers included within the boxes indicate the normal use range.
4. Remember that Marsh funnel viscosities are estimates of Brookfield viscosity, good to about ±200 centipoise.

Table 22.—Marsh funnel time—Brookfield viscosity relationship for forest fire retardant solutions[1] (use with procedure 7)

Time for 1 quart to flow through funnel[2]	Large tip[3]							Small tip[4]			
	PC A	PC D75	PC XB	FT GTS	FT 100	FT 931	M 2700	FK IIP	PC 259	PC G	FT STP
Min:sec	Centipoise										
0:14					758						
16					1086						
18	503				1341		492				
20	676	572	457	485	1545		645				
22	832	817	596	611	1712		785				
24	975	1021	723	727	1851		912				
26	1106	1194	839	834	1969		1029				
28	1227	1342	948	932	2070		1137			20	
30	1340	1470	1048	1024	2157		1237			26	
32	1446	1583	1142	1110	2233		1332			33	
34	1545	1682	1231	1190	2301		1420		17	41	
36	1639	1770	1314	1266	2361		1504	16	26	51	
38	1727	1849	1393	1338	2415		1583	52	35	63	
40	1811	1920	1468	1407	2463		1658	84	44	76	18
42	1891	1984	1539	1471	2507		1729	113	54	91	43
44	1967	2042	1607	1533	2546		1797	139	63	109	65
46	2040	2095	1672	1592	2583		1862	163	72	128	86
48	2110	2144	1734	1649	2616		1924	186	81	150	105
50	2177	2189	1793	1703	2646		1983	206	90	175	122
52	2241	2231	1851	1755	2675		2041	225	100	203	138
54	2303	2269	1906	1806	2701		2096	242	109	233	152
56	2362	2305	1959	1854	2725		2149	258	118	267	166
58	2420	2338	2010	1901	2748		2200	273	127	305	179
1:00	2475	2369	2059	1946	2769	1900	2250	287	136	346	191
02	2529	2398	2107	1989	2789		2297	300	145	391	202
04	2581	2425	2153	2032	2807		2344	313	155	440	212
06	2632	2450	2198	2073	2824		2389	324	164	494	222
08		2474	2242	2112	2841		2432	335	173	552	231
10		2497	2284	2151	2856		2475	345	182	615	240
12		2519	2325	2188	2871		2516	355	191	683	248
14		2539	2365	2225	2885		2556	364	201		256
16		2558	2404	2260	2898		2595	373	210		263
18		2576	2442	2295	2910		2633	381	219		270
20		2593	2479	2328	2922			389	228		277
22		2610	2525	2361	2933			396	237		283
24			2550	2393	2945			403	246		289
26			2584	2425	2954			410	256		295
28			2618	2455	2964			417	265		301
30				2485	2973			423	274		306
32				2514	2982			429	283		311
34				2543	2990			434	292		316
36				2571	2998			440	302		320
38				2598	3006			445	311		325
40				2625				450	320		329
42								455	329		333
44								459	338		337
46								464	347		341
48								468	357		344
50								472	366		348
52								476	375		351
54								480	384		354
56								484	393		357
58								487	402		360
2:00						2200		491	412		363
02								494	421		366
04								497	430		369
06								500	439		372
08									448		374
10									458		377
3:00						2500					
4:00						2800					
5:00						3100					

[1]Brookfield model LVF viscometer, at 60 r/min, spindle 2 (for viscosities from 1-500 cP) or spindle 4 (for viscosities greater than 500 cP); at 70-80 °F; higher temperature may give false low readings; lower temperatures may give false high viscosities.
[2]Funnel must be full to screen before test begins.
[3]Inside diameter should be 0.269 ± 0.002 inch.
[4]Inside diameter should be 0.187 ± 0.002 inch.
[5]The boxed areas indicate the normal use ranges.

rocedure 9: Determining the Specific Veight of a Fire Retardant by onventional Weight/Volume leasurements

The specific weight of a retardant is calculated from he weight of an accurately known volume of solution. If container of known volume is not available, one can be alibrated by adding a known weight of water to an vailable container and marking the fluid level.

1. Accurately weigh an empty container (1 cup to 1 uart) that has a precisely known volume (such as a itchen measure) on a small scale, such as a postal or itchen scale. The capacity of the scale will determine he size container to use. (The note at the end of this rocedure gives directions for determining the volume of container.)
2. Fill the weighed container to the volume mark with he retardant to be tested. Be sure air bubbles have been llowed to escape first.
3. Weigh the filled container.
4. Subtract the weight of the empty container. This ives the weight of a known volume of retardant.
5. Convert ounces to decimal fractions of pounds by ividing the number of ounces by 16; for example:

   2 lb 4 oz = 2.25 lb (2 + 4/16)

   2 lb 8½ oz = 2.53 lb (2 + 8.5/16)

6. Determine the specific weight using table 23 (appen- ix 3) or calculate the specific weight of the retardant by ıultiplying the weight obtained in step 5 by the ppropriate factor:

Volume weighed	Factor
1 cup	16
2 cups (1 pint)	8
4 cups (1 quart)	4

For example, if 1 quart (4 cups) of retardant weighs lb 3 oz or 2.19 lb, the specific weight is 2.19 × 4 = .76 lb/gal. If 1 cup of retardant weighs 9 oz or 0.56 lb, he specific weight is 0.56 × 16 = 8.96 lb/gal.

IOTE: A narrow-mouth container is preferable to a ride-mouth container. If such a container is not availa- le, one can be made from any appropriately sized arrow-mouth container.

1. Accurately weigh a clean, dry container.
2. Add sufficient water to the container to increase he weight as shown:

Approximate size container	Weight added
	Ounces
1 cup	8
1 pint (2 cup)	16
1 quart (4 cup)	32

3. Mark the fluid level.
4. Empty and dry container and repeat at least three imes.
5. Use a fine-tipped waterproof marker to mark fluid ne.

Procedure 10: Determining the Specific Weight of a Fire Retardant Using a Mud Balance

The Baroid mud balance is designed especially for measuring specific weight. (Other similar instruments may be suitable.) The special container is filled with the material being tested and then placed on the stand and the slide adjusted to balance. Specific weight can be read directly from the built-in scale.

1. Fill the cup attached to the balance with the retardant to be tested.
2. Tap cup until air bubbles are removed (see note below).
3. Seat lid firmly on cup, being sure that some retardant goes through hole. (This ensures that the cup is filled to capacity.)
4. Wipe outside of cup and lid to remove any retardant adhering to container.
5. Place balance on the base with knife edges on the fulcrum rest.
6. Move slide until balance is level.
7. Read the specific weight in pounds per gallon of retardant directly at the edge of the slide nearest the fulcrum.

NOTE: If all entrapped air is not removed the specific weight measured will be less than the specific weight of the retardant itself. Depending on the use of this value, incorrect conclusion may result. For example, the specific weight of a retardant with entrapped air included would be appropriate when the concern is the weight loaded onto an aircraft; however, that same value would not be suitable for quality control purposes such as determining retardant salt content.

Procedure 11: Determining the Specific Weight of a Fire Retardant Using a Hand-Held Density Meter

A sample of the material to be tested is injected into the instrument sample tube. During density measurements the tube oscillates and the internal electronics of the instrument uses the characteristics of the oscillation and several internal constants to automatically calculate and display density. Specific weight can be calculated from the density or it can be looked up directly, in the conversion table provided.

1. Turn density meter on. (Mettler DMA 35; other instruments may be suitable; follow manufacturer's operating instructions.)
2. Fill the sample tube by slowly injecting retardant from a hypodermic syringe into the right-hand nozzle. For unthickened retardants, the sample can be sucked into the sample tube through a tube attached to the left-hand nozzle by squeezing the long rubber bulb on the right side of the meter and then releasing.
3. If there are air bubbles in the sample tube, slowly inject more retardant until all air bubbles are gone.

4. Allow temperature (shown on the meter face) to stabilize.

5. Read density and temperature directly in windows on the meter face.

6. Use table 24 (appendix 3) to convert density (g/mL) to specific weight (lb/gal).

7. Flush sample tube with clean water.

NOTE: Freshly mixed or recirculated samples contain large numbers of small air bubbles that will cause inaccurate density readings. To obtain the true density of the retardant solution it may be necessary to wait overnight for all entrapped air to escape.

Procedure 12: Determining Retardant Salt Content Using a Hand-Held Density Meter

A sample of the material to be tested is injected into the instrument sample tube. During density measurements the tube oscillates and the internal electronics of the instrument uses the characteristics of the oscillation and several internal constants to calculate and display density and temperature automatically. If the test material was pretreated as appropriate for retardant type, the density can be looked up in the salt content tables and salt content read directly.

1. Pretreat the retardant sample as described in procedures 3, 4, or 5 as appropriate for the thickener type.

2. Turn density meter on. (Mettler DMA 35; other instruments may be suitable; follow manufacturer's operating instructions.)

3. Suck the treated sample into the sample tube by squeezing the rubber bulb on the side of the meter, inserting the inlet tube into the sample, and then releasing the rubber bulb.

4. Allow the temperature (shown on the meter face) to stabilize.

5. Read the density and temperature directly in windows on the meter face.

6. Use table 25 (appendix 3) to convert degrees Celsius to degrees Fahrenheit.

7. Correct density reading for temperatures less than 75 °F or greater than 85 °F using table 26 (appendix 3) or the following rule: For every 5 °F the retardant solution temperature is below 80 °F, subtract 0.001 from the hydrometer reading; or for every 5 °F the retardant solution is above 80 °F, add 0.001 to the hydrometer reading.

8. Look up the corrected density reading in the left-hand column of the proper salt content table (2-11) and read the salt content.

9. Flush sample tube with clean water.

NOTE: Freshly mixed retardant samples contain a large number of small air bubbles that will cause inaccurate density readings. If the retardant is to be filtered or treated with viscosity reducing agent, the entrapped air will be unlikely to cause inaccuracies. However, before making corrections to mixed retardant, the sample densities should be verified by retesting after the retardant has been allowed to sit for several hours or overnight.

Procedure 13: Determining Fire Retardant Salt Content Using a Hand-Held Refractometer

When light is focused through a drop of retardant, the light is deflected by an amount that is proportional to the amount of salt present. This deflection is measured on the arbitrary scale built into the refractometer. (American Optical Scientific Instruments model 1440, with a scale from 0 to 30 arbitrary units. Other instruments may also be used, but calibration tables for the specific instrument may be needed.) Using calibration tables provided, retardant salt content can be read directly from this scale reading.

1. Clay-thickened products should be filtered and a drop of clear filtrate used for this test. All other retardants can be used without pretreatment.

2. Lift the instrument cover plate to expose the prism.

3. Using the dipstick provided, or a plastic stirring rod, place one or two drops of the sample on the face of the prism and close the cover. The retardant should form a thin layer covering nearly the entire prism for best results. Avoid use of an excessive amount of retardant as this can give an inaccurate reading.

4. Point the instrument toward a strong light source. Natural light outdoors is best.

5. Look through the eyepiece and read the value where the light/dark line intersects the scale. Tilting the refractometer with respect to the light source may sharpen the contrast and improve readability.

6. Clean the prism and cover plate with a damp cloth or soft tissue. Dry thoroughly.

7. Refer to the appropriate table to convert the scale reading to retardant salt content.

NOTE: Although variations in solution temperature do not affect the accuracy of the refractometer, variations in the temperature of the refractometer itself may do so. To minimize this problem, store the refractometer between 60 °F and 85 °F. Low temperatures cause greater variation than do high temperatures.

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APPENDIX 1: GLOSSARY

Component - any portion of a mixed retardant that is shipped or handled separately in the mixing or delivery procedures.

Corrosion - result of reaction between a metal and its environment.

Density - the mass of substance per unit of volume, grams per milliliter.

Deterioration - the loss of viscosity over time; specifically, for evaluation purposes, any loss of more than 40 percent of the initial viscosity within 1 year after preparation of the solution.

Elasticity - the property of a material enabling it to resist deformation by stretching or pulling apart. Usually used in reference to the cohesiveness or ability of material to hold together during a drop.

Flow conditioner - chemicals that, in very small quantities, tend to prevent other powders from caking. Imparts free flowing qualities to powder.

Inhibitor - any agent that retards a chemical reaction. In retardant applications, usually refers to a viscosity loss inhibitor (bactericide) or corrosion inhibitor.

Liquid concentrate - a retardant concentrate in liquid form, which when diluted with water by simple mixing, forms a mixed retardant.

Long-term retardant - a chemical that has the ability to reduce or inhibit combustion (burning) after the water it originally contained has evaporated. The most common chemical salts used in long-term retardants are ammonium sulfate (AS), monoammonium phosphate (MAP), diammonium phosphate (DAP), and ammonium polyphosphate (APP).

pH - a measure of the acidity or alkalinity of a liquid, on a scale from 0 to 14, with 7 representing neutrality. The lowest numbers are the most acidic and the highest numbers are the most alkaline (basic).

Retardant - a substance that by chemical or physical action reduces or inhibits flammability of combustibl Rate-of-spread of flame front is thereby slowed or retarded.

Rheologic properties - all those physical/chemical properties that influence the fluid flow characteristics of a substance. Viscosity and elasticity are principal rheological properties used to characterize retardant behavior.

Short-term retardant - a substance that relies on the moisture it contains to reduce or inhibit combustion and that is ineffective once its moisture has evaporated. Water and thickened water are short-term retardants.

Slurry - any mixed retardant as it is used operationall normally used to refer to thickened retardants in the viscous state.

Specific weight - weight, in pounds, of 1 gal of substance.

Steady-state viscosity - the viscosity of a retardant 24 hours after initial mixing and that is expected to be maintained for an appreciable time period (week or more).

Thickener - a substance that when added to a liquid ac to increase the viscosity and/or elasticity of that liqu

Viscosity - the internal resistance of a liquid to flow when a defined force is exerted upon it. The viscosity of retardants is normally measured with a Brookfield viscometer or a Marsh funnel.

Viscosity reducing agent - a substance (usually an enzyme) that is added to a gum-thickened retardant t eliminate enough of the viscosity that a hydrometer can be accurately floated in the product.

.PPENDIX 2: TESTING EQUIPMENT .ND SOURCES

For all tests, a clean container (approximately 1 gal) r transferring samples from the retardant mixing and orage area to the test area should be set aside exclu- vely for test purposes.

Viscosity - for all thickened retardants

A. Marsh Funnel Method

1. Marsh funnel (#201) - Baroid. Must be modified for use with fire retardants. Instructions for modification may be obtained from Intermountain Fire Sciences Laboratory, Missoula, MT.

2. Stand and support (S-78306-A and S-19150) - Sargent-Welch Scientific.

3. 1-quart container - local kitchen supply.

4. Thermometer, readable to 1 °F (S-80015-A) - Sargent-Welch Scientific.

5. Stopwatch, watch with second hand, or other timer readable in seconds.

B. Brookfield Viscometer Method

1. Brookfield viscometer and stand (model LVF) - Brookfield Engineering Laboratories.

2. Thermometer, readable to 1 °F (S-80015-A) - Sargent-Welch Scientific.

3. Timer or watch readable to 60 seconds.

Salt Content - all retardants

A. Hydrometer Method

1. Hydrometer of suitable range - Sargent-Welch Scientific.

1.000-1.070 sp. gr. units (S-41885-F)
1.060-1.130 sp. gr. units (S-41885-G)
1.120-1.190 sp. gr. units (S-41885-H)
1.180-1.250 sp. gr. units (S-41885-I)

2. 100-mL graduated cylinder (or 32- by 200-mm test tube and stand) (S-24631-E) - Sargent-Welch Scientific.

3. Thermometer readable to 1 °F (S-80015-A) - Sargent-Welch Scientific.

4.a. Gum-thickened retardants

Viscosity reducing agent - request from C. W. George, Intermountain Fire Sciences Laboratory.

1-quart bottle with lid (S-8416-F) - Sargent-Welch Scientific.

Measuring teaspoon

Watch or other timer

b. Clay-thickened retardants

Filter paper and funnel (or drip coffee filter and holder) (S-35433-F and S-32915-L) - Sargent-Welch Scientific.

Container for filtered solution (S-8416-F) - Sargent-Welch Scientific.

c. Clay-thickened liquid concentrate

Filter paper and funnel (or drip coffee filter and holder) (S-35433-F and S-32915-L) - Sargent-Welch Scientific.

1-quart disposable canteen (8465-00-102-6381) - General Services Administration.

Container for filtered solution (S-8416-F) - Sargent-Welch Scientific.

B. Hand-Held Density Meter Method

1. Density meter (DMA35) - Mettler Instrument Co.

2.a. Gum-thickened retardants

Viscosity reducing agent - request from C. W. George, Intermountain Fire Sciences Laboratory.

1-quart bottle with lid (S-8416-F) - Sargent-Welch Scientific.

Measuring teaspoon

Watch or other timer

b. Clay-thickened retardant

Filter paper and funnel (or drip coffee filter and holder) (S-35433-F and S-32915-L) - Sargent-Welch Scientific.

Container for filtered solution (S-8416-F) - Sargent-Welch Scientific.

c. Clay-thickened liquid concentrate

Filter paper and funnel (or drip coffee filter and holder) (S-35433-F and S-32915-L) - Sargent-Welch Scientific.

1-quart disposable canteen (8465-00-102-6381) - General Services Administration.

Container for filtered solution (S-8416-F) - Sargent-Welch Scientific.

C. Refractometer Method

1. Industrial fluid tester (model 10440) - VWR Scientific.

2. Clay-thickened retardants and liquid concentrates

Filter paper and funnel (or drip coffee filter and holder) (S-35433-F and S-32915-L) - Sargent-Welch Scientific.

Container for filtered solution (S-8416-F) - Sargent-Welch Scientific.

III. Specific Weight - all retardants

A. Weight/Volume Method

1. Container (1 cup to 1 quart size)

2. Kitchen or postal scale

B. Mud Balance Method

1. Baroid mud balance (4-scale model) - Baroid Division.

C. Density Meter Method

1. Hand-held density meter (DMA 35) - Mettler Instrument Co.

Source of Supplies:

1. Baroid Division, National Lead Co., P.O. Box 1675, Houston, TX.

2. Brookfield Engineering Laboratories, 240 Cushing St., Stoughton, MA 02072.

3. General Services Administration, Building 41, Denver Federal Center, Denver, CO 80225.

4. Mettler Instrument Co., P.O. Box 71, Hightstown, NY 08520.

5. Intermountain Fire Sciences Laboratory, RWU-4402, P.O. Box 8089, Missoula, MT 59807.

6. Sargent-Welch Scientific Co., 4040 Dahlia St., P.O. Box 7196, Denver, CO 80207.

7. VWR Scientific, P.O. Box 1004, Norwalk, CA 90650.

APPENDIX 3: TABLES FOR ADJUSTMENT, CORRECTIONS, AND CONVERSIONS

Table 23.—Conversions from weight of a known volume of retardant to specific weight (use with procedure 9)

Net weight of container of retardant		
1 cup	1 quart	Specific weight
		Lb/gal
8 oz	2 lb	8.0
8⅛ oz	2 lb ½ oz	8.13
8¼ oz	2 lb 1 oz	8.25
8⅜ oz	2 lb 1½ oz	8.33
8½ oz	2 lb 2 oz	8.50
8⅝ oz	2 lb 2½ oz	8.63
8¾ oz	2 lb 3 oz	8.75
8⅞ oz	2 lb 3½ oz	8.83
9 oz	2 lb 4 oz	9.0
9 ⅛ oz	2 lb 4½ oz	9.13
9¼ oz	2 lb 5 oz	9.25
9⅜ oz	2 lb 5½ oz	9.33
9½ oz	2 lb 6 oz	9.50
9⅝ oz	2 lb 6½ oz	9.63
9¾ oz	2 lb 7 oz	9.75
9⅞ oz	2 lb 7½ oz	9.83
10 oz	2 lb 8 oz	10.0

Table 24.—Conversion from retardant density to specific weight[1] (use with procedure 11)

Density[2]	Specific weight
g/mL	*Lb/gal*
1.010	8.4
1.022	8.5
1.034	8.6
1.046	8.7
1.058	8.8
1.070	8.9
1.082	9.0
1.094	9.1
1.106	9.2
1.118	9.3
1.130	9.4
1.142	9.5
1.154	9.6
1.166	9.7
1.178	9.8
1.190	9.9
1.202	10.0

[1]At 80 °F. At lower solution temperatures, the tabulated values will be low; at higher solution temperatures, the tabulated value will be high.

[2]For densities outside the values shown or at temperatures other than 80 °F, the conversion can be made by multiplying the density × constant. The constant depends on the solution temperature:

Temperature, °F	Constant
70	8.327
75	8.322
80	8.317

Table 25.—Conversion of temperatures from degrees Celsius to degrees Fahrenheit[1] (use with procedure 6)

Degrees Celsius	Degrees Fahrenheit
4	39
6	43
8	46
10	50
12	54
14	57
16	61
18	64
20	68
22	72
24	75
26	79
28	82
30	86
32	90
34	93
36	97
38	100

[1]For values not given in the table, the temperature in °F can be calculated by: °F = 9/5 × °C + 32.

Table 26.—Adjustments to specific gravity for temperature deviations

Retardant temperature, °F	Correction to specific gravity reading
43-47	subtract 0.007
48-52	subtract .006
53-57	subtract .005
58-62	subtract .004
63-67	subtract .003
68-72	subtract .002
73-77	subtract .001
78-82	no correction needed
83-87	add .001
88-92	add .002
93-97	add .003
98-102	add .004
103-107	add .005
108-112	add .006

APPENDIX 4: SAMPLE CALCULATIONS

I. Sample Calculation to Determine Increase in Volume During Mixing of a Retardant

A. Mixed Retardant from a Dry Chemical

The density of water and two values for the specific retardant (mix ratio and specific weight) are needed for the calculation.

Using Phos-Chek A as an example:

Mix ratio = 0.96 lb of dry chemical/gal of water

Specific weight of the mixed retardant = 8.78 lb/gal of mixed retardant

Specific weight of water (75 °F) = 8.322 lb/gal

Using these values, assume that dry retardant is added to 1 gal of water:

Weight of the mixed retardant

= 0.96 lb of powder + 8.322 lb of water

= 9.282 lb of mixed retardant

From the weight and specific weight of the mixed retardant, calculate the volume of retardant made:

$$\text{Volume} = \frac{9.282 \text{ lb of mixed retardant}}{8.78 \text{ lb/gal of mixed retardant}}$$

$$= 1.0572 \text{ gal of mixed retardant}$$

The percentage increase in volume is calculated using the amount of water added as a base:

$$\text{Percentage increase} = \frac{(1.0572 - 1.00)100}{1.00} = 5.72\%$$

To calculate the amount of powder needed to make 1 gal of retardant, divide the amount of powder added to 1 gal of water by the total volume of mixed retardant:

Weight of powder/gal of retardant

$$= \frac{0.96 \text{ lb of powder/gal of water}}{1.0572 \text{ gal of retardant}}$$

$$= 0.908 \text{ lb of powder/gal of retardant}$$

This figure can be used to figure retardant yield per ton of powder.

In this example:

$$\text{Yield} = \frac{2{,}000 \text{ lb/ton}}{0.908 \text{ lb of powder/gal of retardant}}$$

$$= 2{,}203 \text{ gal of retardant/ton of powder}$$

B. Mixed Retardant from a Liquid Concentrate

The calculations are similar when using a liquid concentrate, but an additional value, the specific weight of the concentrate, is needed.

Using Fire-Trol 931 as an example:

Mix ratio = 4:1 (4 parts water to 1 part concentrate)

Specific weight of concentrate = 11.78 lb/gal

Specific weight of mixed retardant = 9.15 lb/gal

Specific weight of water (75 °F) = 8.322 lb/gal

Using these values, assume that 0.25 gal of liquid concentrate is added to 1 gal of water:

Weight of mixed retardant

$$= \frac{11.78 \text{ lb/gal of concentrate}}{4} + 8.322 \text{ lb/gal of water}$$

$$= 2.945 + 8.322 = 11.267 \text{ lb of mixed retardant}$$

From the weight and specific weight of the mixed retardant, calculate the volume of retardant made:

$$\text{Volume} = \frac{11.267 \text{ lb of mixed retardant}}{9.15 \text{ lb/gal of mixed retardant}}$$

$$= 1.2314 \text{ gal of mixed retardant}$$

The percentage increase in volume is calculated using the amount of water added as a base:

$$\text{Percentage increase} = \frac{(1.2314 - 1.00)100}{1.00} = 23.14\%$$

To calculate the amount of concentrate needed to make 1 gal of mixed retardant, divide the weight of concentrate added to 1 gal of water by the volume of mixed retardant made:

Weight of concentrate/gal of retardant

$$= \frac{2.945 \text{ lb of concentrate/gal of water}}{1.2314 \text{ gal of retardant}}$$

$$= 2.392 \text{ lb of concentrate/gal of retardant}$$

Similarly, to calculate the volume of concentrate needed to make 1 gal of retardant, divide the volume of concentrate added to 1 gal of water by the volume of mixed retardant made:

Volume of concentrate/gal of mixed retardant

$$= \frac{0.25 \text{ gal of concentrate/gal of water}}{1.2314 \text{ gal of retardant}}$$

$$= 0.203 \text{ gal of concentrate/gal of retardant}$$

These figures can be used to calculate retardant yield per ton of concentrate or per tanker load of concentrate:

$$\text{Yield} = \frac{2{,}000 \text{ lb/ton}}{2.392 \text{ lb of concentrate/gal of mixed retardant}}$$

$$= 836 \text{ gal of mixed retardant/ton of concentrate}$$

$$\text{Yield} = \frac{5{,}000 \text{ gal/tanker}}{0.203 \text{ gal of concentrate/gal of mixed retardant}}$$

$$= 24{,}631 \text{ gal of mixed retardant}$$

II. Salt Content of Mixed Retardant

A. Calculate the Salt Content of a Mixed Retardant from a Liquid Concentrate

When the mix ratio (such as 4:1) of the retardant made from a liquid concentrate is known, the salt content can be calculated provided that the density (or specific weight [sp. wt.]) and salt content of the concentrate are known.

For example: Fire-Trol 931-L concentrate has a salt content of 31.8% P_2O_5 and specific weight of 11.96 lb/gal. If the concentrate is diluted 4:1 with water (assume 4 gal of water are mixed with 1 gal of a concentrate), what is the salt content of the mixed retardant?

(con.)

Weight of P_2O_5

= (sp. wt. of concentrate) × (percent of salt in concentrate)

= 11.96 × 0.318

= 3.80 lb of P_2O_5

Weight of mixed retardant

= weight of 1 gal of concentrate + weight of 4 gal of water

= 11.96 + 4 × 8.32

= 11.96 + 33.28

= 45.24 lb of mixed retardant

Salt content of mixed retardant

$$= \frac{\text{weight of } P_2O_5 \text{ in mixed retardant}}{\text{weight of mixed retardant}} \times 100$$

= (3.80/45.24) × 100

= 8.4% P_2O_5

B. To Calculate the Salt Content of a Mixed Retardant from a Dry Powder

When the mix ratio of a product made from a powder and the salt content of that powder are known, the salt content of the mix retardant can be calculated.

For example: Phos-Chek 259 is made by mixing 1.14 lb of powder with 1 gal of water. If the powder has a salt content of 90.5% diammonium phosphate (DAP), what is the salt content of the resulting mixed retardant?

Weight of DAP

= (weight of powder used) (percent salt)

= (1.14)(0.905)

= 1.03 lb of DAP

Weight of mixed retardant

= weight of powder + weight of water

= 1.14 + 8.32

= 9.46 lb of mixed retardant

Salt content of mixed retardant

$$= \frac{\text{weight of DAP}}{\text{weight of mixed retardant}} \times 100$$

$$= \frac{1.03}{9.46} \times 100$$

= 10.9% DAP

To convert percentage DAP to percentage P_2O_5 for direct comparisons of salt content divide by 1.86:

$$\text{Percent } P_2O_5 = \frac{\%\ \text{DAP}}{1.86}$$

$$= \frac{10.9}{1.86}$$

= 5.9% P_2O_5 in mixed retardant

APPENDIX 5: SAMPLE RECORDKEEPING FORMS

Not all forms are suitable for all bases. Nor are these examples intended to be all inclusive. The particular situation at each base and the type of retardant used will be the primary factors in determining the forms needed.

Example 1.—Liquid concentrate (fill out for each truckload).

Date of delivery ____________________ Time of delivery ____________________

Retardant name ____________________

Volume of delivery ____________________ (Specify pounds or gallons)

Bill of lading (or other identification) number ____________________

Name and address of supplier:

Lot acceptance information:

Hydrometer reading: ______________ at ______________°F (temperature)

Additional identification ____________________

Quality assurance program:

Was sample sent to designated collection point? __________ (yes/no)

Additional identification ____________________

Comments: (If liquified at the base, volume of water used; any obvious settling or solids; appearance out of the ordinary; if this truckload was added to material already in storage, estimate volume and salt content of the material in storage, if more than one storage tank is used, specify where new material is added, etc.)

Example 2.—Liquid concentrate summary (one line for each addition of material).

Tank identification: ______________________________

Delivery		Amount liquified or added		Specific gravity in tank		Sample identification
Date	Time	lb	gal	before mixing	after mixing	

Example 3.—Retardant mixing data (for batch mixing—fill out for each batch or eductor mix from Phos-Bin, etc.).

Date of mix ______________________ Time of mix ____________________________

Volume of water used ______________________ (gal)

Amount of dry material or concentrate used _________________________ (lb/gal)

Marsh funnel time __________ min and _________ sec at _________ °F (temperature)

Viscosity: ________________________ centipoise
(or Brookfield viscometer spindle) ____________ × ____________ (factor)

Hydrometer reading: ____________ at ____________ °F (temperature)

Reading corrected for temperature _________________________

Salt content: ____________ % ____________ (specify salt)

Was a correction made? ________________ (yes/no)

If yes: Amount of water/retardant added __________________

Hydrometer reading (after correction): ________________ at ____________ °F

Reading corrected for temperature __________________

Salt content: ________________ % ________________ (specify salt)

Is this batch being used for lot acceptance? ______________________________

Was quality assurance sample sent to proper collection point? ___________ (yes/no)

Additional identification ______________________________________

Comments: (how mixed, appearance other than usual, etc.)

Example 4.—Mixed retardant storage data (to track retardant in tanks, test weekly).

Tank identification ______________________

Test date	Test time	Specific gravity	Temperature, °F	Corrected sp. gr.	Salt content	Marsh funnel time minutes and seconds	Viscosity Centipoise	Comments[1]

[1]Comments as to sample history, such as material held from last season; tanks being closed until next season; sample sent to collection point for testing, etc.

Example 5.—Retardant slurry data (for retardant mixed and pumped directly to airtanker).

Sample date	Sample time	Marsh funnel time (min & sec)	Viscosity (Centipoise)	Hydrometer reading	Slurry temperature (°F)	Corrected hydrometer reading	Field salt content	Comments[1]

[1]Comments as to sample history, such as: loaded into airtanker No. 17; fire name; sample sent to RO.

Example 6.—Information for lot acceptance inspection or other tests.

FOR USE ONLY BY COLLECTION POINT

Sample No. ______________

LOT ACCEPTANCE INSPECTION & TESTS

Retardant Sample

Mixing base name/location: ______________ Amount received: ______________

Retardant product: ______________ Shipper No. ______________

Date/time received: ______________ Packaging damage: Yes ☐ No ☐

Container properly marked: Yes ☐ No ☐ Remarks: ______________

____

____

Sample Information

Date/time mixed, if not LC: ______________ Volume mixed: ______________

Time sample drawn: ______________ Sample taking procedure (how sample drawn, etc.): ______________

____

____

Marsh funnel time: ______________ Viscosity: ______________

Hydrometer reading/temperature: ______________ Salt content: ______________

Name/title/phone (FTS; commercial) of person testing sample: ______________

____

____

____

Original: Collection point — Copy: Retain at base

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George, Charles W.; Johnson, Cecilia W. Determining fire retardant quality in the field. General Technical Report INT-201. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986. 42 p.

Onsite fire retardant effectiveness is dependent on a retardant's physical (rheological) and chemical (active fire-inhibiting salt) properties. Quality control at each retardant base is necessary to assure cost-effectiveness is achieved. Using relatively simple techniques, retardant salt content and viscosity can be monitored in the field to determine quality. This paper describes field procedures for determining retardant quality using calibration tables developed for most long-term and short-term retardants. Corrective actions to bring properties within desired ranges are included.

KEYWORDS: fire suppression, fire retardants, quality control, active chemical, salt content, physical properties, rheology, viscosity, corrective actions, procedures, specific weight

INTERMOUNTAIN RESEARCH STATION

The Intermountain Research Station provides scientific knowledge and technology to improve management, protection, and use of the forests and rangelands of the Intermountain West. Research is designed to meet the needs of National Forest managers, Federal and State agencies, industry, academic institutions, public and private organizations, and individuals. Results of research are made available through publications, symposia, workshops, training sessions, and personal contacts.

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Fire Behavior Computations with the Hewlett-Packard HP-71B Calculator

Ronald A. Susott
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RESEARCH SUMMARY

A Custom Read Only Memory (CROM) has been developed for the Hewlett-Packard model 71B hand-held calculator for fire behavior computations. The calculator replaces the Texas Instruments TI-59. The CROM programs allow many computations not found in the TI-59 version and implement most of the programs in the BURN subsystem of the BEHAVE fire behavior prediction system. An additional metric mode is included in the programs. A separate CROM was developed for computing the 1978 National Fire-Danger Rating (NFDR) indexes and components, and a separate user's manual has been published: Burgan, Robert E.; Susott, Ronald A. Fire Danger Calculations with the Hewlett-Packard HP-71B Calculator. General Technical Report INT-199. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986. 16 p.

This report describes the operation of the HP-71B program for fire behavior predictions, the inputs needed, and outputs calculated for each of 13 separate program modules. Sample worksheets are included and worked examples are given for each module of the program.

CONTENTS

Fire Behavior Computations with the Hewlett-Packard HP-71B Calculator

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NTRODUCTION

The Hewlett-Packard HP-71B has been selected to ›place the Texas Instruments TI-59 (Burgan 1979) for eld computations of fire danger and fire behavior. This ıanual describes operation of the fire behavior programs s implemented on the HP-71B. The programs are ıtended for field use by fire behavior analysts who are ımiliar with the methods for gathering input data, for ıterpreting program outputs, and for applying these ata to fire problems. Rothermel (1983) has described ıe methods needed to predict fire behavior. Operation f a separate program written for fire danger rating pplications is described in a companion publication 3urgan and Susott 1986). Each program is available as separate Custom Read Only Memory (CROM).

Separate self-study guides have been prepared for the re danger and fire behavior programs. These are availa-le through your agency coordinator, who will distribute ıe guides and help answer questions about the calcula-ɔr and the course material.

The HP-71B fire behavior program is patterned after ıe BURN subsystem of the BEHAVE fire behavior rediction and fuel modeling system (FIRE1 and FIRE2 rograms). The keywords, program organization, line umbers, and worksheets are similar to those of EHAVE. The majority of the papers describing the URN subsystem (Andrews 1986) describe the models sed for the calculations, their limitations, and applica-ons. Technical references given there are not repeated ere. It is strongly recommended that the reader be ımiliar with those papers.

'ALCULATOR FEATURES

The HP-71B has several features that make it more ıitable for field use than the TI-59 it replaces:

- A liquid crystal display (LCD) that is easy to see in ıylight.
- The capability to display both alphabetic and numeric ıaracters.

his eliminates the need for keyboard overlays because ›quests for input and displayed output can be appropri-ːely labeled.

- Use of complementary metal oxide on semiconductor 'MOS) architecture which, because of its very low ɔwer requirement, permits many hours of operation ›tween battery changes.
- Use of replaceable, rather than rechargeable, batteries.
- A continuous memory that retains the information stored in the calculator even when the calculator is turned off.
- A capability to be used with optional battery-operated printers, data cassettes, and disk drives.
- A powerful BASIC programming language that is available for many other user applications.

PROGRAM FEATURES

The fire behavior program for the HP-71B implements much more fire behavior technology than was possible with the TI-59. Program capabilities are indicated by the following list of program modules and their functions:

- FUEL MODEL - permits inputting, loading, listing model names or values, saving and deleting models.
- DIRECT - calculates spread rate, heat per unit area, fireline intensity, flame length, reaction intensity, effective windspeed, and direction of maximum spread.
- SIZE - calculates area, perimeter, length-to-width ratio, forward spread distance, backing spread distance, and maximum fire width.
- CONTAIN - calculates length of fireline at containment time, time to containment, and final fire size or required line-building rate.
- SPOT - calculates maximum spotting distance.
- SCORCH - calculates scorch height.
- IGNITE - calculates probability of ignition.
- MOISTURE - calculates 1-hour timelag fuel moisture, fuel level temperature and relative humidity, percentage of area shaded, and probability of ignition for either a specific burn time or as hourly calculations.
- MAP - calculates fire dimensions, spread distance, and maximum spot distance for plotting on a map.
- SLOPE - calculates slope steepness, elevation change, and horizontal distance.
- WIND - calculates midflame windspeed from the windspeed measured 20 feet above the general vegetation surface.
- RH - calculates relative humidity and dew point.
- TWO - calculates weighted rate of spread for the two-fuel-model concept.
- PRINTER - not a module, but provides the option of directing output to a printer.

The 13 standard fire behavior fuel models (Anderson 1982) are included in the CROM. Up to 19 additional user-defined fuel models (numbered 14-99) can also be

entered, and stored in the calculator memory. The fuel modeling subsystem of BEHAVE (Burgan and Rothermel 1984) is strongly advised for the development and testing of user models before their entry into calculator memory.

The program has a metric version that provides for both metric inputs and outputs. Separate data sheets are provided for the English and the metric versions. These data sheets are at the end of this report.

Operation of the fire behavior program will not alter any values assigned to variables created in other programs and saved in continuous memory. Some global flags and system characteristics such as DELAY, OPTION BASE, DEG/RADIANS, Display Format, and Round-off Setting are changed by the program and not reset. User programs that need these system flags or characteristics should be written to correctly initialize them. Refer to the HP-71 Reference Manual for more detailed information.

Operation of the BEHAVIOR program uses a large portion of the HP-71B memory. Large user files or previously defined variables can cause the "Insufficient Memory" error at unpredictable locations in the program. The "DESTROY ALL" statement may reclaim enough memory to run the program, or files can be removed with the "PURGE" statement. Users who frequently have large files in memory should consider obtaining the optional memory expansions available for the HP-71B.

PROGRAM STRUCTURE

When BEHAVIOR is run, the program first enters the MAIN module. The MAIN module's only function is to call other modules that actually perform the desired calculations. Figure 1 shows that the structure of these other modules is divided into three levels. The first le[vel] is called directly from MAIN, and the modules in level 1 can be run independent of other modules. Once calcula[tions] tions have been made in a level 1 module, that module can call the next level and pass calculated outputs to [it]. The called level is said to be "linked" to the calling mod[-] ule through the information passed. For example, a DIRECT-SIZE-CONTAIN run will pass DIRECT outputs to SIZE and both DIRECT and SIZE outputs to CONTAIN. The run outputs from a module can be passed to any of the modules available for linking. For example, level 2 SIZE outputs can be linked to MAP to convert the spread distances to map distances. When MAP is Quit and the program returns to SIZE, a link[ed] CONTAIN uses the same outputs from the last SIZE run to calculate containment times. All outputs of a module Run are valid until new inputs are made or th[e] module is Quit. Modules shown in figure 1 that canno[t] call other modules cannot pass outputs to any other module. For example, the 1-hour moisture calculated b[y] the MOISTURE module cannot be passed to DIREC[T]. Of course, such a calculated moisture can be manuall[y] entered when running the DIRECT module.

Modules are selected through use of their two-letter keywords—the underlined letters in the module name [in] figure 1. Additional, generally single letter, keywords [are] used to perform specific tasks within each module. Th[e] large ENDLINE key is used to complete all user entri[es]. Once a module is selected, its keywords are operative and will appear in the display. The Quit keyword is u[se]d to move one level to the left in figure 1. Each level m[u]st be Quit to return to the MAIN level where you can select another module or Quit the program.

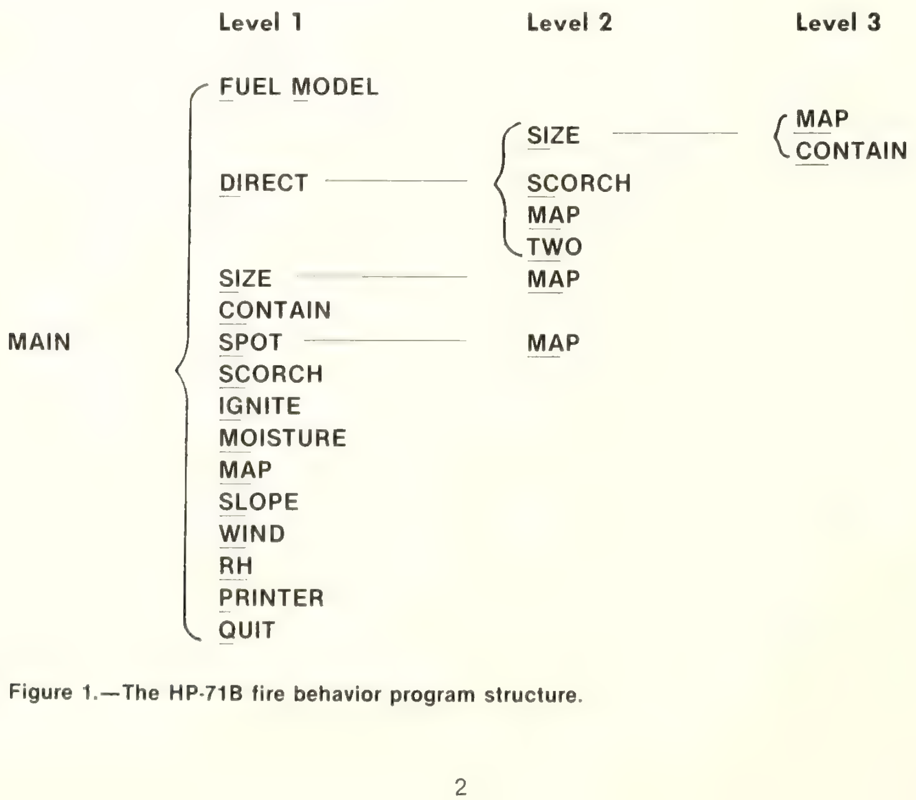

Figure 1.—The HP-71B fire behavior program structure.

GENERAL PROGRAM OPERATION

Operation of the MAIN Section

After the HP-71B has been turned on, the fire behavior program can be started in either of two ways:

1. Type in RUN BEHAVIOR and press the ENDLINE key. This will always start the program at the beginning.
2. If the fire behavior program was the last program run before the calculator was turned off, just press the RUN key.

When the program starts running, the letters PRGM will appear in the right side of the display, followed immediately by a short display of the words "FIRE BEHAVIOR". The program then asks whether or not you want the metric version and slope in degrees. Entry of No to these questions, or just pressing ENDLINE, gives the defaults of English version and slope in percent. If a printer is attached, **and turned on**, the message "PRINTER ON" is briefly displayed; otherwise the message "NO PRINTER AVAILABLE" is briefly displayed. Finally, the program indicates you are in the MAIN section by displaying the message "MAIN: FM,DI,SI,SP". This is the MAIN module prompt and the characters following the colon are a menu of keywords for the allowable modules. The remainder of the MAIN section module keywords may be seen by repeatedly pressing the ∧ or the ∨ keys. The other prompts displayed are:

"MAIN: CO,SC,IG,MO";

"MAIN: MA,SL,WI,RH";

"MAIN: P,Q".

The display sequence repeats if the ∧ or ∨ keys are pressed several times. When you are in the MAIN section you can go to one of the modules, set the Printer to on or off, or Quit by entering the appropriate keyword and pressing ENDLINE. The keyword does not have to be currently displayed. Any incorrect entry will just disappear when you press ENDLINE and you can try again.

Normal termination of the fire behavior program is by using the keyword Quit when you are in the MAIN section. You may turn the calculator off any time the program waits for user input, by pressing the gold f ON to invoke the "OFF" command. The calculator will also automatically turn off if there is no activity for about 10 minutes. In these last cases, when the calculator is turned back on, the SUSP annunciator will appear in the display indicating program operation is now suspended. The best way to continue from this point is to press the gold f + for the "CONT" or continue command and a question mark "?" will appear. This indicates the program is still waiting for input of the item being requested when the calculator was turned off. If you do not know what to enter, press the + key (or any nonnumeric), then press ENDLINE, and the display will prompt for the requested input. Pressing the RUN key, or entering "RUN BEHAVIOR", will restart a suspended program from the beginning and previous work will be lost. Failure to end the program by quitting from MAIN will result in abnormal functioning of some calculator keys.[1] If this happens, enter "RUN BEHAVIOR" and Quit when the display reads "MAIN: FM,DI,SI,SP?". This will return the calculator to normal operation.

Input and Output Procedures

The program will not accept values outside a reasonable range assigned to each item. Although the program does limited checking of the completeness of the inputs, you should be certain the inputs are correct before doing any computations. On the other hand, inputs that do not change from run to run only need to be entered once. If there is any question as to whether or not the inputs are correct, they should be listed before the program is run.

All the modules employ the same techniques for data entry and modification. The inputs for each module have been numbered (see data sheets) and arranged in a specific sequence.

All inputs are initialized to −100 each time you start the program by entering "RUN BEHAVIOR" or by pressing the RUN key. If you do a series of runs, previously defined inputs will remain, thus **always** list your inputs and check their values before calculating outputs. The program will prompt for those inputs needed by the module being run and check whether or not a value has been entered for all required inputs. Valid inputs are limited to reasonable ranges as shown with the input prompt and listed on the data sheets. If you attempt to enter nonvalid data, it will simply disappear from the display and you may try again. If you have entered an input and it appears that the calculator is not proceeding, the reason is that your input was probably outside the permissible range and you are being asked again for the same input. In general, inputs to one module are not passed to other modules at the same level; exceptions are the fuel model number and map inputs common to MAP and SLOPE.

ENTERING AND LISTING INPUTS

To enter or list input items, you can:

- begin inputting or listing data at the first item in the list by entering I or L, respectively, followed by an ENDLINE. This is the normal procedure for input and will ensure that all needed entries are made.
- begin inputting or listing data at any item number by entering I# or L# respectively, where # is the item number (as shown on the data sheets). A space between L and # is optional. For example, entering I4 when the display reads "DIRECT: I,L,R,Q?" will allow entry of 100H moisture (fourth item in the DIRECT list).

Once you have started entering input data at some point in the input list, the program continues sequentially down the input list. Entry of inputs can be terminated at any time by pressing ENDLINE without first keying in an entry. This will not affect the input parameter whose value is being requested.

[1]The program uses key files named KEY0, KEY1, and KEY2. Do not use these names for any other purpose.

The program permits entry of only one value for some input items, but 1, 2, or 3 values may be entered for others. Single value items are indicated in the calculator display, by parentheses ( ) surrounding the valid range. These items also have only one entry line on the data sheets. Multiple value items are indicated in the display by square brackets [ ] surrounding the valid range. These items have three entry lines on the data sheets. Multiple values are entered by keying in each number, separated by a comma;[2] that is, 4, 6, 8 and pressing ENTER. Thus, depending on the inputs specified, you can obtain:

- a single output value for each output item by entering only one value for each input item
- a list of 2 or 3 output values for each output item by entering 2 or 3 values for one of the input items
- a table of up to 9 output values for any one of the output items by entering 2 or 3 values for two of the input items.

Input listing can be started at any point by entering L#. If no printer is attached, the display pauses after each line is shown. Subsequent items can be listed by pressing the ∨ key. Previous items can be listed by pressing the ∧ key. Terminate the listing by pressing ENDLINE. When a printer is attached, there is no pause between list items; all remaining items will be printed without pressing any keys.

Values can be input with more decimal places than shown on the listings. The values listed are rounded to fit on the display, but the full precision of the numbers entered is used for calculations. Numbers that must be integers, however, are truncated by the program. For example, if a CONTAIN run option of 1.8 is entered, it will be changed to 1.0.

CHANGING INPUTS

The value of individual input items can be changed by entering I# where # is the number of the input parameter to be changed. The display will show that you are to enter the value for the item requested. Enter the value and press ENDLINE. The next input item will then appear in the display, but if you do not want to change its value, just press ENDLINE.

CORRECTING ERRONEOUS INPUTS

Erroneous entries or typing errors can be corrected before the ENDLINE key is pressed by:

1. Holding down the gold f key and either pressing the < key repeatedly, or holding the < key down. This invokes the "BACK" command printed in gold letters on the calculator. The last entries are deleted by this operation.
2. Pressing or holding the < key to back up the cursor, then deleting the unwanted characters by pressing or holding the gold f key and then the > key. This invokes the "−CHAR" command.
3. By using the < key to back up the cursor, then typing in the correct inputs. If extra characters remain, they can be deleted individually by using the "−CHAR" command or replaced by using spaces.

Refer to the HP-71B Owner's Manual for more detailed line-editing instructions.

OBTAINING OUTPUTS

After you are certain the input values are correct, outputs may be obtained by:

- Entering R (for RUN) to start at the beginning of the output list.
- Entering R# to start at the location of the item number specified. This is normally used to review the value of **specific** output items after completing a valid run.

At the start of a run, the input list is checked. If the inputs are not complete when a run is attempted, the calculator will beep and display the message "INCOMPLETE INPUT". In this case, list the inputs to discover which inputs still have a value of −100, then enter correct values.

If more than two input items are assigned multiple values, the error message "EXTRA MULTI-INPUTS" is displayed. In this case, list your inputs to find which one can be assigned a single value.

After a valid run, the output listing starts automatically. If you are not using a printer, you may scroll up or down the output list by repeatedly pressing the ∧ or ∨ keys, respectively. Output listing is terminated by pressing ENDLINE. If the output is going to a printer, the ∧, ∨, and ENDLINE keys are deactivated and the list is printed from your starting point to the end of the list.

List output is produced (two or three columns for each output), by assigning two or three values to one input item. The first line displayed is the labeled input line for which multiple values were input. Press the ∨ key to display the labeled output line. The output line consists of: the output line number, the mnemonic label, and the two or three output values. After recording the outputs, press the ∨ key to continue. At times the output line can contain more than 22 characters and the first few characters will scroll off the display.

A table is produced by assigning two or three values to each of two input items. You must select the table entry item by its output number "TABLE #(Ø -N)" where N is the number for the last output item for the module you are in. The output numbers are given in the data sheets. For example, entry of 4 for table number when you are in the DIRECT module will produce a table of flame lengths—DIRECT output item 4. Entry of Ø will terminate the table listing, as will ENDLINE with no entry.

The first line of table output consists of four items that identify the table being produced. These are table number, table item, row item, and column item. Refer to the DIRECT module data sheet for the following example. An example display for a flame length table in DIRECT is: 4 FL 1H * MFWS. This identifies the output item to be displayed in the body of the table as output number 4, which is flame length (FL). Each row will be for a different 1-hour timelag fuel moisture (1H) and

[2] Only specific input values can be entered into the calculator, rather than the beginning value, ending value, stepsize as in BEHAVE. For the calculator, the values can be entered in any order.

each column for a different midflame windspeed (MFWS). Enter this type of information above the dashed line across the "table" form at the end of the worksheets.

The next display line, obtained by pressing the ∨ key once, is the input values for the column item. An example display is 6 8 11. Enter this type of output on the three lines **above** the words "Table Values."

The next three output lines are of the form—row number: row value column 1 column 2 column 3 values. An example display of—1:4.0 8.3 10.3 13.2 indicates that for row 1 which has an input value of 4, the table values are 8.3, 10.3, and 13.2 The row number is prerecorded on the data sheet form. Enter the remaining values for each row as you obtain them by pressing the ∨ key to scroll down the outputs. You may also scroll up through the outputs by pressing the ∧ key. Continue scrolling until the module label and keywords reappear, for example, "DIRECT: I,L,R,Q?".

If output is being directed to a printer, separator lines (= = = = =) will be printed to help distinguish the input from the output. If a printer is not being used, these lines will only flash briefly on the display. As with other lists, the entire table is printed without using the scroll keys.

The calculator makes as many "RUNS" as necessary for the number of outputs you requested; that is, one run for a single set of outputs, up to nine runs for a 3 × 3 table containing nine output values. The "RUN" number is displayed as each "RUN" starts. All runs are completed before any outputs are available for listing. Several modules require lengthy calculations and some patience is needed while the runs are being completed.

OPERATING THE MODULES "INDEPENDENTLY"

The FUEL MODEL Module

The purpose of this module is to permit entry of a site-specific **fire behavior** fuel model into calculator memory. It is strongly advised that such models be developed and tested through use of the FUEL subsystem of BEHAVE before entering them into the calculator. (See Burgan and Rothermel [1984] for detailed information on developing fuel models.) Fire behavior cannot be calculated with this module—it is strictly for managing and maintaining a file of user fuel models.

When the calculator display shows—"MODEL: G,I,L,S,Q?"—you are in the fuel model module. Pressing the ∧ key shows an alternate prompt "MODEL: LM,DM" for additional menu selections. While in the fuel model module, you may:

- Get a standard model (numbered 1-13) or a site-specific fire behavior fuel model (numbered 14-99) by entering G and a number. For example, you can get model 14—if it has been previously entered and saved—by keying in G14 and pressing ENDLINE. If the requested model is available, the display will show "MODEL # LOADED", where # is the requested model number. If the model is not available, the message "MODEL # NOT FOUND" is displayed and another input requested. Alternatively, you can just enter G and the calculator will then request a model number.
- Input all the data for a new model by entering I when the display shows—"MODEL: G,I,L,S,Q?". The program recognizes that some inputs are not always required. For example, if the WOODY LOAD is entered as zero, the WOODY S/V ratio input will not be requested. HERB TYPE and HERB S/V ratio are similarly linked to HERB LOAD. Individual parameters can be input or changed by referring to their line numbers. For example, I3 will cause the calculator to request a value for 1HR LOAD, the third item in the FUEL MODEL input list. This procedure will allow input of herbaceous and WOODY S/V ratios and HERB TYPE even if they are not needed. The values assigned to unneeded inputs are saved in the user fuel model files, but they have no effect on calculations.
- List the current values from the beginning (by entering L) or from any other location in the list by entering a line number with the L, for example, L3, and repeatedly pressing the ∨ or ∧ keys.
- Save a model in the user model files, which the program automatically creates for you.[3] If you just Get an existing model from the file and try to Save it without renumbering it, the calculator will beep, briefly display the fact that the model already exists, then ask if you want to "KILL OLD XX (Y/N)?" where XX is the model number. This gives you the options of replacing the existing fuel model (Y), or not saving the model (N). Entering N avoids replacing an existing fuel model with the same number. The model number can be changed to an unused number before saving. When a model is successfully saved, the display will read "MODEL # SAVED", where # is the model number. Up to 19 models can be filed with any model number from 14 to 99. The order of entry of different model numbers is not important; for example, model 99 can be entered and saved first. An attempt to save more than 19 models will result in an error message "USER FILE IS FULL" and the model will not be saved. The way to save the model at this point is to either change the model number to that of an existing user model (which is no longer needed), or to delete one of the existing models (see below). You can get models 1 to 13 and make changes, but they can only be saved if the model number is changed to 14 to 99. The program prompts for a model number in the correct range and a name before completing the Save operation.
- List Models to obtain a list of all the models in the user model files, by number and name. A message "NO USER MODELS" will be displayed if the file is empty. Scroll up and down through the list with the ∧ and ∨ keys. The contents of the file may be recorded in the form provided after the Fuel Model Module form.
- Delete Models allows you to delete individual fuel models from the file. When the display reads "DELETE MODEL (14-99)?" enter the number of the model to be

[3]Up to four model files are automatically created in memory, named: USERMOD0, USERMOD1, USERMOD2, and USERMOD3. These names should not be purged or used for other purposes.

deleted. If that model is not in the file, you will get the message "MODEL # NOT FOUND" and another request for the number of the model to be deleted. If the model you want to delete is in the file, the display will read "DELETE # (Y/N)?". If you enter Y, the model will be deleted from the file and another model number requested. Terminate deletions by pressing ENDLINE with no model number entered in the display.

• Quit to exit the fuel model module. If a valid model is not present when Quit is selected, the error message "INCOMPLETE INPUT" is displayed. The program will not Quit the fuel model module until the model has all needed inputs. List will show a −100 for missing inputs. User fuel models should normally be Saved before quitting this section, although a temporary fuel model can be entered and used for calculations in other modules. Any fuel model you Get or build in this module will also be assigned to any other module requiring a fuel model. The normal procedure is to assign fuel models as required by each module you operate.

The DIRECT Module

The prompt "DIRECT: I,L,R,Q" indicates that you are in the DIRECT module. An alternate DIRECT menu "DIRECT: SI,SC,MA,TW" is displayed by pressing the up arrow, ∧ , when the module prompt is shown. These modules can be linked to DIRECT after a valid Run is made, as discussed later.

The DIRECT module provides five outputs that describe the general characteristics of the fire (1 through 5). The effective windspeed (6) is for the direction of the spread calculation, whether or not that is the direction of maximum spread rate. If either the slope or windspeed is greater than Ø , the input of spread direction (input item 10) is preceded by the question: "PREDICT AT MAX (Y/N)?". If the answer is N, item 10 is requested, but if the answer is Y, item 10 is not entered and all predictions will be in the direction of maximum spread. The direction of maximum spread (7) is output if predictions are in the direction of maximum spread. A list of inputs will show a "MAX" for spread direction whenever the calculations are made in the direction of maximum spread rate. Exhibit 1 shows three runs that provide typical examples of using the DIRECT module. A table of values for any other DIRECT output could also be generated from the input list in exhibit 1c. Exhibit 1e shows a printer list for the above examples: The format for the printer output is the same as display output without a printer.

DIRECT MODULE (English Units)

LIST NUMBER 22a

(Keywords: Input, List, Run, Quit, SIze, SCorch, MAp, TWo)

IPUT (Input, List)

1	MODEL #	Fuel model number	(1-99)		3	
2	1H	1-H fuel moisture	[1-60%]	6.0		
3	10H	[1]10-H fuel moisture	[1-60%]	—		
4	100H	[1]100-H fuel moisture	[1-60%]	—		
5	HERB	[1]Live herb moisture	[30-300%]	—		
6	WOOD	[1]Live woody moisture	[30-300%]	—		
7	MFWS	Midflame windspeed	[0-99 mi/h]	8		
8	SLP	Slope	[0-100% or 0-45 degrees]	30%		
9	WDIR	[2]Direction of wind vector, deg. clockwise from uphill	[0-360 degrees]	20		
	PREDICT AT MAX		(Y/N)		Y	
10	SDIR	Direction of spread calc., deg. clockwise from uphill (or from wind vector if slope is zero)	[0-360 degrees]			MAX

UTPUT (Run)

0		No more tables				
1	ROS	Rate of spread	ch/h	228		
2	H/A	Heat per unit area	Btu/ft^2	742		
3	FLI	Fireline intensity	Btu/ft/s	3,102		
4	FL	Flame length	ft	18.2		
5	RI	Reaction intensity	Btu/ft^2/min	2,900		
6	EWS	Effective windspeed in direction SDIR	mi/h	8.4		
7	MAXD	[3]Direction of maximum spread, deg. clockwise from uphill	degrees	19		

ıput only if corresponding fuel load is not zero.
ıput only if midflame windspeed (MFWS) and slope (SLP) are not zero.
ıutput only if calculations are in direction of maximum spread.

xhibit 1a.—DIRECT run obtaining a single set of outputs.

DIRECT MODULE (English Units)

LIST NUMBER 226

(Keywords: Input, List, Run, Quit, SIze, SCorch, MAp, TWo)

INPUT (Input, List)

1	MODEL #	Fuel model number	(1-99)		3	
2	1H	1-H fuel moisture	[1-60%]	6.0	9.0	12.0
3	10H	[1]10-H fuel moisture	[1-60%]	–		
4	100H	[1]100-H fuel moisture	[1-60%]	–		
5	HERB	[1]Live herb moisture	[30-300%]	–		
6	WOOD	[1]Live woody moisture	[30-300%]	–		
7	MFWS	Midflame windspeed	[0-99 mi/h]	8		
8	SLP	Slope	[0-100% or 0-45 degrees]	30%		
9	WDIR	[2]Direction of wind vector, deg. clockwise from uphill	[0-360 degrees]	20		
	PREDICT AT MAX		(Y/N)		N	
10	SDIR	Direction of spread calc., deg. clockwise from uphill (or from wind vector if slope is zero)	[0-360 degrees]	10		

OUTPUT (Run)

0		No more tables				
1	ROS	Rate of spread	ch/h	189	155	13
2	H/A	Heat per unit area	Btu/ft^2	742	673	64
3	FLI	Fireline intensity	Btu/ft/s	2,574	1,912	1,62
4	FL	Flame length	ft	16.7	14.5	13.
5	RI	Reaction intensity	Btu/ft^2/min	2,900	2,628	2,5
6	EWS	Effective windspeed in direction SDIR	mi/h	7.3	7.3	7.3
7	MAXD	[3]Direction of maximum spread, deg. clockwise from uphill	degrees	–	–	–

[1]Input only if corresponding fuel load is not zero.
[2]Input only if midflame windspeed (MFWS) and slope (SLP) are not zero.
[3]Output only if calculations are in direction of maximum spread.

Exhibit 1b.—DIRECT run obtaining a list of outputs for a range of three 1-hour moisture inputs.

DIRECT MODULE (English Units)

LIST NUMBER 22c

(Keywords: Input, List, Run, Quit, SIze, SCorch, MAp, TWo)

INPUT	(Input, List)					
1	MODEL #	Fuel model number	(1-99)		3	
2	1H	1-H fuel moisture	[1-60%]	6.0	9.0	12.0
3	10H	[1]10-H fuel moisture	[1-60%]	–		
4	100H	[1]100-H fuel moisture	[1-60%]	–		
5	HERB	[1]Live herb moisture	[30-300%]	–		
6	WOOD	[1]Live woody moisture	[30-300%]	–		
7	MFWS	Midflame windspeed	[0-99 mi/h]	8		
8	SLP	Slope	[0-100% or 0-45 degrees]	30%		
9	WDIR	[2]Direction of wind vector, deg. clockwise from uphill	[0-360 degrees]	20		
	PREDICT AT MAX		(Y/N)		N	
10	SDIR	Direction of spread calc., deg. clockwise from uphill (or from wind vector if slope is zero)	[0-360 degrees]	10	60	110
OUTPUT	(Run)					
0		No more tables			See output table on next page.	
1	ROS	Rate of spread	ch/h			
2	H/A	Heat per unit area	Btu/ft^2			
3	FLI	Fireline intensity	Btu/ft/s			
4	FL	Flame length	ft			
5	RI	Reaction intensity	$Btu/ft^2/min$			
6	EWS	Effective windspeed in direction SDIR	mi/h			
7	MAXD	[3]Direction of maximum spread, deg. clockwise from uphill	degrees			

[1]Input only if corresponding fuel load is not zero.
[2]Input only if midflame windspeed (MFWS) and slope (SLP) are not zero.
[3]Output only if calculations are in direction of maximum spread.

Exhibit 1c.—DIRECT input list for a range of three values for two inputs.

OUTPUT TABLES

LIST NUMBER 22 d

TABLE NO. 6 TABLE ITEM: EWS ROW ITEM 1H COL. ITEM SDIF

Row No.	Row Value	Column Values: 10	60	110
		Table Values		
1	6.0	7.3	2.2	0.6
2	9.0	7.3	2.2	0.6
3	12.0	7.3	2.2	0.6

TABLE NO. ______ TABLE ITEM: ______ ROW ITEM ______ COL. ITEM ______

Row No.	Row Value	Column Values:		
		Table Values		
1				
2				
3				

TABLE NO. ______ TABLE ITEM: ______ ROW ITEM ______ COL. ITEM ______

Row No.	Row Value	Column Values:		
		Table Values		
1				
2				
3				

Exhibit 1d.—Table of effective windspeed outputs for the range of three values for two inputs shown in exhibit 1

```
1  MODEL  #          3          Ex. 1a
2  1H    6.0
7  MFWS  8
8  SLP   30
9  WDIR  20
10 SDIR             MAX

======================

1  ROS   228
2  H/A   742
3  FLI   3102
4  FL    18.2
5  RI    2900
6  EWS   8.4
7  MAXD  19

======================


1  MODEL  #          3          Ex. 1b
2  1H    6.0   9.0   12.0
7  MFWS  8
8  SLP   30
9  WDIR  20
10 SDIR  10

======================
   1H    6.0   0.0   12.0
======================
1  ROS   189   155   136
2  H/A   742   673   648
3  FLI   2574  1912  1620
4  FL    16.7  14.5  13.5
5  RI    2900  2628  2532
6  EWS   7.3   7.3   7.3
======================


1  MODEL  #          3          Ex. 1c
2  1H    6.0   9.0   12.0
7  MFWS  8
8  SLP   30
9  WDIR  20
10 SDIR  10    60    110

======================
  6  EWS    1H    *  SDIR
         10    60    110
======================
1:6.0    7.3   2.2   0.6        Ex. 1d
2:9.0    7.3   2.2   0.6
3:12.0   7.3   2.2   0.6
======================
```

Exhibit 1e.—Printer list for examples of DIRECT module.

The SIZE Module

The prompt "SIZE: I,L,R,MA,Q" indicates that you are in the SIZE module operating independently (not linked to DIRECT). The SIZE module provides estimates of the fire size, perimeter, length-to-width ratio, forward and backing spread distances, and maximum width at the end of a specified burning time. These estimates are for a fire originating from a point source, not a line source, and spreading at a constant rate through surface fuels during the elapsed time. The fire shape is assumed to be approximately elliptical. Exhibits 2a, 2b, and 2c illustrate typical runs in the SIZE module.

SIZE MODULE (English Units)

LIST NUMBER 23a

(Keywords: Input, List, Run, MAp, [1]COntain, Quit)

INPUT	(Input, List)					
1	ROS	[2]Rate of spread	[0.1-500 ch/h]	20.0		
2	EWS	[2]Effective windspeed	[0-99 mi/h]	8.0		
3	ET	Elapsed time	[0.1 - 8 h]	1.0	2.0	4.0
OUTPUT	(Run)					
0		No more tables				
1	AREA	Area	acres	11	44	178
2	PER	Perimeter	ch	46	92	183
3	L/W	Length-to-width ratio		3.0	3.0	3.0
4	FSD	Forward spread distance	ch	20.0	40.0	80.0
5	BSD	Backing spread distance	ch	0.6	1.2	2.4
6	MXW	Maximum fire width	ch	6.9	13.7	27.5

[1]SIZE can link to CONTAIN only if linked to DIRECT.
[2]Input only when SIZE is used as an independent module.

Exhibit 2a.—SIZE run obtaining a list of outputs for a range of elapsed burning time inputs.

SIZE MODULE (English Units)

LIST NUMBER 23b

(Keywords: Input, List, Run, MAp, [1]COntain, Quit)

INPUT	(Input, List)					
1	ROS	[2]Rate of spread	[0.1-500 ch/h]	5.0	10.0	20.0
2	EWS	[2]Effective windspeed	[0-99 mi/h]	8.0		
3	ET	Elapsed time	[0.1 - 8 h]	1.0	2.0	4.0
OUTPUT	(Run)					
0		No more tables		see output table on next page.		
1	AREA	Area	acres			
2	PER	Perimeter	ch			
3	L/W	Length-to-width ratio				
4	FSD	Forward spread distance	ch			
5	BSD	Backing spread distance	ch			
6	MXW	Maximum fire width	ch			

[1]SIZE can link to CONTAIN only if linked to DIRECT.
[2]Input only when SIZE is used as an independent module.

Exhibit 2b.—SIZE input list for generating a table of outputs.

OUTPUT TABLES

LIST NUMBER 23b

TABLE NO. 1 TABLE ITEM: AREA ROW ITEM ROS COL. ITEM ET

Row No.	Row Value	Column Values: 1.0	2.0	4.0
		Table Values		
1	5.0	1	3	11
2	10.0	3	11	44
3	20.0	11	44	178

TABLE NO. 2 TABLE ITEM: PER ROW ITEM ROS COL. ITEM ET

Row No.	Row Value	Column Values: 1.0	2.0	4.0
		Table Values		
1	5.0	11	23	46
2	10.0	23	46	92
3	20.0	46	92	183

TABLE NO. ______ TABLE ITEM: ______ ROW ITEM ______ COL. ITEM ______

Row No.	Row Value	Column Values:		
		Table Values		
1				
2				
3				

Exhibit 2c.—SIZE output tables of areas and perimeters calculated from the inputs in exhibit 2b.

The CONTAIN Module

The CONTAIN module is used to estimate fire suppression requirements, providing the following two run options for this purpose:

- Run option 1—estimate the total line-building rate required to contain the fire at a specific size, called the burned area target.
- Run option 2—estimate the final fire size, given a specific line-building capability.

Either run option permits the fire to be attacked at the head or the rear.

The results from CONTAIN are valid only within the basic assumptions that were used in developing the mathematical model. These are:

- The fire has an elliptical shape at the time of attack.
- The rate of spread is constant during the time required to construct the control line.
- The containment line is constructed at the edge of the fire.
- Work proceeds simultaneously on both sides of the fire at an equal pace.

CONTAIN MODULE (English Units)

LIST NUMBER 25a

(Keywords: Input, List, Run, Quit)

INPUT	(Input, List)					
1	RUN OPT	Run option 1 = calculate total line building rate 2 = calculate burned area	(1 or 2)		1	
2	ATTACK OPT	Attack option 1 = head 2 = rear	(1 or 2)		1	
3	ROS	[1]Rate of spread	[0.1-500 ch/h]	10.0	15.0	20.0
4	AREA	[1]Initial fire area	[0.1-100 acres]	5.0		
5	L/W	[1]Length-to-width ratio	[1-5]	3.0		
6	BAT	[2]Burned area target	[0.1-2000 acres]	7.0		
7	TLBR	[3]Total line-building rate	[0.1-800 ch/h]	—		
OUTPUT	(Run)					
1	PER	Total length of line	chains	35	35	35
2	TIME	Containment time	hours	1.0	0.7	0.5
3	FFS	[4]Final fire size	acres	—	—	—
3	TLBR	[5]Total line-building rate	ch/h	33	50	67
4	MAXA	[5]Maximum area calculable	acres	8	8	8
5	MINA	[5]Minimum area calculable	acres	5	5	5

Error Codes:

−1 = Burned area target too large, cannot calculate slow enough line building rate
−2 = Line building rate too slow to catch fire
−3 = L/W ratio too large
−4 = Burned area target too close to initial fire size
−5 = Line building rate too fast

[1]Input only when CONTAIN is used as an independent module.
[2]Input only for run option = 1 (calculate total line-building rate).
[3]Input only for run option = 2 (calculate burned area target).
[4]Output only for run option = 2.
[5]Output only for run option = 1.

Exhibit 3a.—CONTAIN run obtaining a list of outputs using run option 1.

When calculating the final fire size, CONTAIN uses otal line-building rate rather than line-building rate per lank as was used in the TI-59 program (Albini and Chase 1980). The program then applies half of the line-building rate to each flank. Thus the line-building rate ntered must be more than twice the forward rate of spread; otherwise the control forces will never catch the ire.

When calculating the line-building rate required to contain the fire to a specific size, the target fire size must e larger than the initial fire size.

Calculator results from this module may differ somewhat from the BEHAVE outputs because the computational algorithm is different. To save computation time, the calculator results are based on a table lookup and interpolation process, whereas BEHAVE uses a pure computational method (Andrews and Morris in preparation). Because it is easy for the value of requested outputs to exceed the limits of the table in the calculator, the maximum (MAXA) and minimum (MINA) burned area targets calculable are output (Run option 1). Negative numbers (−1 to −5) indicate error codes as referenced on the data sheet. Exhibits 3a and 3b provide examples of calculating both total line-building rate and final fire size.

CONTAIN MODULE (English Units)

LIST NUMBER 25b

(Keywords: Input, List, Run, Quit)

INPUT	(Input, List)					
1	RUN OPT	Run option 1 = calculate total line building rate 2 = calculate burned area	(1 or 2)		2	
2	ATTACK OPT	Attack option 1 = head 2 = rear	(1 or 2)		2	
3	ROS	[1]Rate of spread	[0.1-500 ch/h]	10.0	15.0	20.0
4	AREA	[1]Initial fire area	[0.1-100 acres]	5.0		
5	L/W	[1]Length-to-width ratio	[1-5]	3.0		
6	BAT	[2]Burned area target	[0.1-2000 acres]	–		
7	TLBR	[3]Total line building rate	[0.1-800 ch/h]	60.0		
OUTPUT	(Run)					
1	PER	Total length of line	chains	47	62	94
2	TIME	Containment time	hours	0.8	1.0	1.6
3	FFS	[4]Final fire size	acres	10	15	30
3	TLBR	[5]Total line building rate	ch/h	–		
4	MAXA	[5]Maximum area calculable	acres	–		
5	MINA	[5]Minimum area calculable	acres	–		

Error Codes:

−1 = Burned area target too large, cannot calculate slow enough line building rate
−2 = Line building rate too slow to catch fire
−3 = L/W ratio too large
−4 = Burned area target too close to initial fire size
−5 = Line building rate too fast

[1]Input only when CONTAIN is used as an independent module.
[2]Input only for run option = 1 (calculate total line building rate).
[3]Input only for run option = 2 (calculate burned area target).
[4]Output only for run option = 2.
[5]Output only for run option = 1.

Exhibit 3b.—CONTAIN run obtaining a list of outputs using run option 2.

The SPOT Module

The SPOT module predicts the **maximum** spotting distance from three firebrand sources:

- torching trees
- burning piles
- wind-driven surface fires.

Although spot fires may occur at lesser distances, the purpose of this calculation is to estimate the greatest distance at which spot fires can be expected. The number of spot fires likely to occur is not estimated. None of the spotting calculations apply in the case of extreme fire behavior such as running crown fires, or any situation in which large fire whirls occur.

The wind-driven surface fire option applies only to fires occurring in surface fuels without timber cover and predicts only intermediate range spotting. Specifically not included is short-range (a few tens of yards) spotting resulting from low intensity fires, or very long-range (several miles) spotting associated with extreme fire behavior such as crowning and large fire whirls.

Exhibits 4a, 4b, and 4c provide an example of input required for each of the three firebrand sources.

SPOT MODULE (English Units)

LIST NUMBER 26a

(Keywords: Input, List, Run, MAp, Quit)

INPUT	(Input, List)					
1	BRAND SRC	Firebrand source 1 = torching trees 2 = burning piles 3 = wind-driven surface fire	(1-3)		1	
2	MCHT	Mean cover height	[0-300 ft]	100		
3	20'W	20-ft windspeed	[0-99 mi/h]	10	20	40
4	RVEL	Ridge-to-valley elevation difference	[0-4,000 ft]	1,500		
5	RVHD	Ridge-to-valley horiz. distance	[0-4 mi]	1.5		
6	SRC LOC	Spotting source location 0 = midslope, windward side 1 = valley bottom 2 = midslope, leeward side 3 = ridgetop	(0-3)		3	
7	TREE SP	[1]Tree species 1 = Engelmann spruce 2 = Douglas-fir, subalpine fir 3 = hemlock 4 = ponderosa, lodgepole pine 5 = white pine 6 = balsam fir, grand fir	(1-6)		2	
8	DBH	[1]Torching tree DBH	[5-40 inches]	20		
9	TRHT	[1]Torching tree height	[10-300 ft]	90		
10	#TR	[1]Number of torching trees	[1-30]	4		
11	FLHT	[2]Continuous flame height	[1-100 ft]	–		
12	FL	[3]Flame length	[0.1-50 ft]	–		
13	MODEL #	[3]Fuel model	(1-99)		–	
14	HERB	[4]Herbaceous moisture	[30-300%]	–		
OUTPUT	(Run)					
1	SPOT	Maximum spotting distance	mi	0.24	0.47	0.88

[1]Input only for firebrand source = 1 (torching tree option)
[2]Input only for firebrand source = 2 (burning pile option)
[3]Input only for firebrand source = 3 (wind-driven surface fire option)
[4]Input only for dynamic fuel models with a herbaceous fuel load

Exhibit 4a.—SPOT run with torching trees as the firebrand source.

SPOT MODULE (English Units)

LIST NUMBER 26b

(Keywords: Input, List, Run, MAp, Quit)

INPUT (Input, List)

1	BRAND SRC	Firebrand source 1 = torching trees 2 = burning piles 3 = wind-driven surface fire	(1-3)		2	
2	MCHT	Mean cover height	[0-300 ft]	100		
3	20'W	20-ft windspeed	[0-99 mi/h]	10	20	40
4	RVEL	Ridge-to-valley elevation difference	[0-4,000 ft]	1,500		
5	RVHD	Ridge-to-valley horiz. distance	[0-4 mi]	1.5		
6	SRC LOC	Spotting source location 0 = midslope, windward side 1 = valley bottom 2 = midslope, leeward side 3 = ridgetop	(0-3)		3	
7	TREE SP	[1]Tree species 1 = Engelmann spruce 2 = Douglas-fir, subalpine fir 3 = hemlock 4 = ponderosa, lodgepole pine 5 = white pine 6 = balsam fir, grand fir	(1-6)		–	
8	DBH	[1]Torching tree DBH	[5-40 inches]	–		
9	TRHT	[1]Torching tree height	[10-300 ft]	–		
10	#TR	[1]Number of torching trees	[1-30]	–		
11	FLHT	[2]Continuous flame height	[1-100 ft]	20		
12	FL	[3]Flame length	[0.1-50 ft]	–		
13	MODEL #	[3]Fuel model	(1-99)		–	
14	HERB	[4]Herbaceous moisture	[30-300%]	–		

OUTPUT (Run)

1	SPOT	Maximum spotting distance	mi	0.09	0.18	0.35

[1]Input only for firebrand source = 1 (torching tree option).
[2]Input only for firebrand source = 2 (burning pile option).
[3]Input only for firebrand source = 3 (wind-driven surface fire option).
[4]Input only for dynamic fuel models with a herbaceous fuel load.

Exhibit 4b.—SPOT run with burning piles as the firebrand source.

SPOT MODULE (English Units)

LIST NUMBER 26c

(Keywords: Input, List, Run, MAp, Quit)

INPUT	(Input, List)					
1	BRAND SRC	Firebrand source 1 = torching trees 2 = burning piles 3 = wind-driven surface fire	(1-3)		3	
2	MCHT	Mean cover height	[0-300 ft]	100		
3	20'W	20-ft windspeed	[0-99 mi/h]	10	20	40
4	RVEL	Ridge-to-valley elevation difference	[0-4,000 ft]	1,500		
5	RVHD	Ridge-to-valley horiz. distance	[0-4 mi]	1.5		
6	SRC LOC	Spotting source location 0 = midslope, windward side 1 = valley bottom 2 = midslope, leeward side 3 = ridgetop	(0-3)		3	
7	TREE SP	[1]Tree species 1 = Engelmann spruce 2 = Douglas-fir, subalpine fir 3 = hemlock 4 = ponderosa, lodgepole pine 5 = white pine 6 = balsam fir, grand fir	(1-6)		—	
8	DBH	[1]Torching tree DBH	[5-40 inches]	—		
9	TRHT	[1]Torching tree height	[10-300 ft]	—		
10	#TR	[1]Number of torching trees	[1-30]	—		
11	FLHT	[2]Continuous flame height	[1-100 ft]	—		
12	FL	[3]Flame length	[0.1-50 ft]	20.0		
13	MODEL #	[3]Fuel model	(1-99)		4	
14	HERB	[4]Herbaceous moisture	[30-300%]	—		
OUTPUT	(Run)					
1	SPOT	Maximum spotting distance	mi	0.33	0.52	0.80

[1]Input only for firebrand source = 1 (torching tree option).
[2]Input only for firebrand source = 2 (burning pile option).
[3]Input only for firebrand source = 3 (wind-driven surface fire option)
[4]Input only for dynamic fuel models with a herbaceous fuel load.

Exhibit 4c.—SPOT run with a wind-driven surface fire as the firebrand source.

The SCORCH Module

The SCORCH module can be used to estimate the height to which tree crowns will be scorched by a surface fire burning beneath them. This module must be used with caution because very limited data were used for development of the mathematical scorch height model. Results may also be erroneous if applied to slopes steeper than 30 percent. Exhibit 5 shows a typical example of a SCORCH module run.

SCORCH MODULE (English Units)

(Keywords: Input, List, Run, Quit)

NPUT	(Input, List)					
1	TEMP	Ambient air temperature	[33-120 °F]	90		
2	FL	[1]Flame length	[0.1-20 ft]	4.0		
3	MFWS	[1]Midflame windspeed	[0-10 mi/h]	0	5	10
)UTPUT	(Run)					
1	SCHT	Scorch height	feet	30	21	10

[1]nput only if SCORCH is used as an independent module.

TABLE NO. 1 TABLE ITEM: Scorch height ROW ITEM ____ COL. ITEM ____

Column Values: ____ ____ ____

Row No.	Row Value	Table Values		
1				
2				
3				

Exhibit 5.—SCORCH run obtaining a list of scorch heights for a range of midflame windspeeds.

The IGNITE Module

The IGNITE module can be used to calculate the probability that a firebrand will ignite a fire if it lands on fine dead fuel. Probability is calculated to the nearest 10 percent and does **not** indicate whether or not the ignition will result in a sustained fire. The probability of ignition is not the same as the ignition component (IC) of the National Fire-Danger Rating System (NFDRS). The NFDRS-IC uses fire spread rate as well as probability of ignition to estimate the likelihood of a sustained fire on which suppression action may be required. The MOISTURE module discussed later also calculates ignition probability.

Exhibit 6 shows an example probability of ignition run.

IGNITE MODULE (English Units)

(Keywords: Input, List, Run, Quit)

INPUT	(Input, List)					
1	TEMP	Ambient air temperature	[33-120 °F]	90		
2	1H	1-h fuel moisture	[1-60%]	5.0	10.0	15.0
3	SHAD	Shade	[0-100%]	30		
OUTPUT	(Run)					
1	P(I)	Probability of ignition	pct	70	30	20

TABLE NO. 1 TABLE ITEM: Prob. of Ignition ROW ITEM ______ COL. ITEM ______

Row No.	Row Value	Column Values:		
		Table Values		
1				
2				
3				

Exhibit 6.—IGNITE run obtaining a list of ignition probabilities for a range of 1-hour fuel moistures.

The MOISTURE Module

The MOISTURE module is used to calculate the moisture content of fine dead fuels (Rothermel and others 1986). It has two run options:

- Run option 1.—Calculate the 1-hour fuel moisture, fuel level temperature and relative humidity, percent shade, and probability of ignition for a specific time. This is the burn time option.
- Run option 2.—Calculate the 1-hour fuel moisture and fuel level temperature and relative humidity each hour. This is the hourly option.

The input line numbers have been made to coincide with those used for the MOISTURE and SITE modules of the FIRE2 program of BEHAVE. Thus, missing input line numbers are for FIRE2 line numbers not used for the HP-71.

Although there are numerous inputs, many are not used for specific cases. For example, aspect is not requested if the slope is 0, timber overstory information is not requested if the crown closure is 0, sunset and sunrise weather are not asked if burn time is before sunset, and the various moisture initialization options request different inputs. These examples are not exhaustive, but the program will prompt for the data required for any specific run.

If you do not have estimates of the overstory tree characteristics and think you can estimate the amount of shade caused by the overstory, answer line 15 (crown closure) with 0 percent and line 25 (burn day cloud cover) with your estimate of shade for both the clouds and the overstory. This is recommended only for option 1.

Several input items are requested for the "burn day," which is defined to be the period from 1200 noon to 1200 noon, **not** from midnight to midnight. "Burn day −1" is the previous period from 1200 to 1200. The amount of weather input required depends on the time of day designated as "burn time."

Fuel moisture must be specified at 1400 on the day before the burn. BEHAVE offers five "Moisture Initialization Options" to assist in specifying this value, but the HP-71B calculator offers only four. Moisture initialization option 2 (complete data for the previous 7 days) is not allowed. Option 1 permits input of fine fuel moisture when it is known for the day before the burn; options 3, 4, and 5 are used when incomplete weather information is available.

Particular care must be exercised when changing the value of specific inputs by entering them individually. You may find that more input is required (the calculator displays "INCOMPLETE INPUTS") or that you are using invalid inputs left over from a previous run. While this is true with all modules, it is particularly true with this one, so **always** list and check your inputs before a RUN.

Examples of RUN OPTION 1 and RUN OPTION 2 are shown in exhibits 7a and 7b. The other inputs are the same for both cases. Enter the input values shown to get the burn time outputs. Then change the first input (RUN OPTION) to 2, and rerun to get the hourly output table. Multiple inputs are not allowed in the hourly option. The MOISTURE module takes longer to run as burn time approaches the end of the burn day or if multiple inputs are used, so some patience is required to obtain an answer in these cases. The output form for run option 2 has an extra line at the bottom to record burn time data that does not end on an even hour.

MOISTURE MODULE (English Units)

LIST NUMBER 30a-1

(Keywords: Input, List, Run, Quit)

INPUT	(Input, List)					
1	RUN OPT	Run option 1 = Burn time calculations 2 = Hourly calculations	(1 or 2)		1	
TIME AND LOCATION						
2	BURN MONTH	Month of burn	(1-12)		7	
3	BURN DAY	Day of burn	(1-31)		12	
4	LATITUDE	Latitude of fire location	(−90 to 90 degrees)		45	
5	BURN TIME	Time of burn	(0-2,359 h)		2,230	
FUEL MODEL						
6	MODEL #	Fuel model number	(1-99)		2	
SLOPE, ELEVATION, ASPECT						
11	SLP	Slope steepness	[0-100% or 0-45 degrees]	20		
12	ELFL	Elevation of fire location	[0-12,000 ft]	3,000		
	RH OBS AT FIRE		(Y/N)		Y	
13	ELOB	Elevation of T&RH observations	(0-12,000 ft)		–	
14	ASPECT	Aspect of fire location 0 = north 180 = south 90 = east 270 = west	(0-360 degrees)		270	
TIMBER OVERSTORY DESCRIPTION						
15	CCLO	Crown closure	[0-100%]	20		
16	FOLIAGE	Foliage presence 0 = absent 1 = present	(0 or 1)		1	
17	SHADE TOL	Shade tolerance 0 = intolerant 1 = tolerant	(0 or 1)		0	
18	DOM TYPE	Dominant tree type 1 = coniferous 2 = deciduous	(1 or 2)		1	
19	AVHT	Average tree height	[10-300 ft]	80		
20	H/H	Crown height/tree height ratio	[0.1-1]	0.50		
21	H/D	Crown height/crown diameter ratio	[0.2-5]	3.00		

Exhibit 7a.—MOISTURE run obtaining just burn time outputs using run option 1.

MOISTURE MODULE (continued, English Units)

LIST NUMBER 30a-2

EARLY AFTERNOON WEATHER

22	14T	Burn day 1400 temperature	[33-120 °F]	80		
23	14RH	Burn day 1400 relative humidity	[1-100%]	20		
24	14W	Burn day 1400 20-ft windspeed	[0-99 mi/h]	10		
25	14CC	Burn day cloud cover	[0-100%]	20		
26	14HZ	Burn day 1400 haziness	[1-4]	2		

1 = very clear sky
2 = average clear forest atmosphere
3 = moderate blue haze
4 = dense haze—moderate smoke

SUNSET WEATHER

27	SST	Sunset temperature	[33-120 °F]	70		
28	SSRH	Sunset relative humidity	[1-100%]	25		
29	SSW	Sunset 20-ft windspeed	[0-99 mi/h]	5		
30	SSCC	Sunset cloud cover	[0-100%]	20		

SUNRISE WEATHER

31	SRT	Sunrise temperature	[33-120 °F]	—		
32	SRRH	Sunrise relative humidity	[1-100%]	—		
33	SRW	Sunrise 20-ft windspeed	[0-99 mi/h]	—		
34	SRCC	Sunrise cloud cover	[0-100%]	—		

BURN TIME WEATHER

35	BTT	Burn time temperature	[33-120 °F]	65		
36	BTRH	Burn time relative humidity	[1-100%]	28		
37	BTW	Burn time 20-ft windspeed	[0-99 mi/h]	4		
38	BTCC	Burn time cloud cover	[0-100%]	—		
39	BTHZ	Burn time haziness	[1-4]	—		

1 = very clear sky
2 = average clear forest atmosphere
3 = moderate blue haze
4 = dense haze—moderate smoke

Exhibit 7a. (Con.)

MOISTURE MODULE (continued, English Units)

LIST NUMBER 30a-3

BURN TIME WIND

40	EXPOSURE	Exposure of fuels to wind 1 = exposed 2 = partially sheltered 3 = fully sheltered—open stand 4 = fully sheltered—dense stand 5 = direct entry of wind adjustment factor	(1-5)		2	
41	WAF	Wind adjustment factor Exposure 5 only	(0-1)		-	

MOISTURE INITIALIZATION OPTION

43	MOIS OPT	Moisture initialization option 1 = fine fuel moisture known for day before burn 2 = not allowed 3 = incomplete data; rain the week before burn 4 = incomplete data; no rain the week before burn 5 = incomplete data; weather pattern changing	(1-5)		1	

MOISTURE OPTION 1

44	FM-1	Burn day −1 fine fuel moisture	[1-100%]	10		

MOISTURE OPTION 3

51	RDAY	Number of days before burn that rain occurred	[1-7 days]	—		
52	RAIN	Rain amount, hundredths of an inch	[0-400]	—		
53	RDT	1400 temperature on rain day	[33-120 °F]	—		
54	SKY CODE	Sky condition from rain day to burn day 1 = clear 2 = cloudy 3 = partly cloudy	(1-3)		—	

MOISTURE OPTION 4

No additional input.

Exhibit 7a. (Con.)

MOISTURE MODULE (continued, English Units)

LIST NUMBER 30a-4

MOISTURE OPTION 5

55	TD-1	Burn day −1 1400 temperature	[33-120 °F]	—		
56	RD-1	Burn day −1 1400 relative humidity	[1-100%]	—		
57	WD-1	Burn day −1 1400 20-ft windspeed	[0-99]	—		
58	CD-1	Burn day −1 1400 cloud cover	[0-100%]	—		
59	WTHR	Weather condition prior to burn day −1 1 = hot and dry 2 = cool and wet 3 = between 1 and 2	[1-3]	—		

OUTPUT (Run)

1	MOIS	1-hour fuel moisture	pct	6.2		
2	TEMP	Fuel level temperature	°F	65		
3	%RH	Fuel level relative humidity	pct	28		
4	SHAD	Percent of area shaded	pct	100		
5	P(I)	Probability of ignition	pct	50		

Exhibit 7a. (Con.)

MOISTURE MODULE (continued, English Units)

LIST NUMBER 30b

HOURLY OUTPUT (Run)

TIME	FMOIST pct	FTEMP °F	FRH pct
14	6.1	88.7	15.0
15	5.8	86.8	16.0
16	5.7	83.4	17.7
17	5.7	79.0	20.0
18	5.7	74.6	22.6
19	5.8	71.6	24.2
20	5.9	69.3	25.4
21	6.1	67.5	26.5
22	6.2	65.8	27.5
23			
24			
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			
11			
Burn Time 22.5	6.2	65.0	28.0

Exhibit 7b.—MOISTURE outputs using the inputs listed in exhibit 7a but with run option 2 to calculate hourly values.

The MAP Module

The MAP module permits calculation of fire spread distances, or spot distances, with the output expressed in units (inches or centimeters) to enable plotting the fire on a map. Inputs of scale option, representative fraction, and inches per mile are common to both MAP and SLOPE modules. In the metric option, only representative fraction is allowed for scale option. Exact output obtained depends on the UNITS OPTION selected and whether the run is independent or linked to other modules.

The example shown in exhibit 8 is for an independent MAP run. Note that unit option 2 (spot distance) requires an input in miles while other inputs are in chains. Also, unit option 3 (rate of spread) requires the elapsed time to make the distance calculation. The input and output characteristics of linked MAP runs vary considerably and will be discussed in a later section.

MAP MODULE (English Units)

LIST NUMBER 3/a

(Keywords: Input, List, Run, Quit)

INPUT (Input, List)						
1	SCL OPT	Scale option 1 = Representative fraction 2 = Inches per mile	(1 or 2)		2	
2	RF/1000	[1]Representative fraction/1,000 e.g., RF of 1/24,000 = 24	(1-500)		—	
3	IN/MI	[2]Inches per mile	(0.0625-8)		2.00	
4	UNITS OPT	Units option 1 = Spread distance 2 = Spot distance 3 = Rate of spread	(1-3)		3	
5	DIST	[3]Spread distance	[0-1000 ch]	—		
6	SPOT	[4]Spot distance	[0.1-10 mi]	—		
7	ROS	[5]Rate of spread	[0.1-500 ch/h]	20.0		
8	TIME	[5]Elapsed time	[0.1-8 h]	1.0	2.0	4.0
5	FSD	[6]Forward spread distance	ch	—		
6	BSD	[6]Backing spread distance	ch	—		
7	MXW	[6]Maximum fire width	ch	—		
OUTPUT (Run)						
1	MFSD	Forward spread distance on map (UNITS OPT = 1 or 3)	inches	0.5	1.0	2.0
1	MSPT	Forward spot distance on map (UNITS OPT = 2)	inches	—		
2	MBSD	Backing spread distance on map (SIZE linked only)	inches	—		
3	MMXW	Maximum fire width on map (SIZE linked only)	inches	—		

[1]Input only for scale option = 1.
[2]Input only for scale option = 2.
[3]Input only for units option = 1.
[4]Input only for units option = 2.
[5]Input only for units option = 3.
[6]Passed from SIZE for linked run only. No input is needed.

Exhibit 8.—MAP run obtaining a list of map distances for forward fire spread distances.

The SLOPE Module

The purpose of the SLOPE module is to provide a convenient means of calculating slope steepness, which you can then input to another module. Slope is output in both percentage and degrees, and does not depend on slope input units selected at the start of the BEHAVIOR program. All the inputs can be obtained from a good contour map. Inputs of scale option, representative fraction, and inches per mile are common to both SLOPE and MAP modules. In the metric option only representative fraction is allowed for scale option. The heading "From Point ___ to ___ Point " on the worksheet is to provide a label that corresponds to similarly labeled points on a map. A typical slope calculation is shown in exhibit 9.

SLOPE MODULE (English Units)

LIST NUMBER 32a

(Keywords: Input, List, Run, Quit)

From Point A to Point B

INPUT (Input, List)

1	SCL OPT	Scale option 1 = Representative fraction 2 = Inches per mile	(1 or 2)	2
2	RF/1000	[1]Representative fraction/1,000 e.g., RF of 1/24,000 = 24	(1-500)	—
3	IN/MI	[2]Inches per mile	(0.0625-8 in)	2.00
4	CON INT	Contour interval	(10-500 ft)	200
5	MAP DIST	Map distance	(0.1-10 in)	1.0
6	# INTVLS	Number of contour intervals	(1-100)	3

OUTPUT (Run)

1	SLP %	Slope steepness	pct	23
2	SLP DEG	Slope steepness	degrees	13
3	EL DIFF	Elevation change	feet	600
4	HORIZ DIST	Horizontal distance	feet	2640

[1]Input only for scale option = 1.
[2]Input only for scale option = 2.

Exhibit 9.—SLOPE run example.

The WIND Module

The WIND adjustment module is used independently to adjust the windspeed, as measured 20 feet above the vegetation, to a windspeed at midflame height. In the metric version, the program assumes the 20-foot windspeed equals the 10-meter windspeed. The midflame windspeed can then be entered manually in other modules. Four wind exposure options are available for various amounts of sheltering, plus a fifth option to enter the wind adjustment factor directly. The adjustment factor for exposed fuels depends on the fuel model; the adjustment factors for sheltered and partially sheltered fuels do not. A typical midflame windspeed calculation is shown in exhibit 10.

WIND ADJUSTMENT MODULE (English Units)

(Keywords: Input, List, Run, Quit)

INPUT	(Input, List)					
1	20'W	20-ft windspeed	[0-99 mi/h]	5	10	15
2	EXPOSURE	Exposure to wind	(1-5)		1	
		1 = exposed 2 = partially sheltered 3 = fully sheltered, open stand 4 = fully sheltered, closed stand 5 = enter wind adjustment factor				
3	WAF	[1]Wind adjustment factor	(0-1)		—	
4	MODEL #	[2]Fuel model number	(1-99)		2	
OUTPUT	(Run)					
1	MFWS	Midflame windspeed	mi/h	2.0	4.0	6.0

[1]Input only for exposure = 5.
[2]Input only for exposure = 1.

Exhibit 10.—WIND run example.

The RH Module

The RH module is used to calculate relative humidity and dew point from dry and wet bulb temperatures, and elevation. The output RH is not automatically passed to other modules, but it can be entered manually. The RH calculations assume ice is present on the wet bulb if the temperature is below 32 °F (0 °C). Dew points below freezing are with respect to liquid water. An error will be generated if you enter a wet bulb temperature greater than the dry bulb temperature or if the dew point temperature is unrealistically low (below −40 °F or −40 °C). A typical humidity calculation is shown in exhibit 11.

RH MODULE (English Units)

(Keywords: Input, List, Run, Quit)

INPUT (Input, List)

1	DRYB	Dry bulb temperature	[33-120 °F]	80	85	90
2	WETB	Wet bulb temperature	[0-120 °F]	70	68	66
3	EL	Elevation	[0-12,000 ft]	5,000		

OUTPUT (Run)

1	%RH	Relative humidity	pct			
2	DEWP	Dew point	°F			

ERROR CODES:

−888 = Wet bulb temperature greater than dry bulb temperature

−999 = Dew point too cold for valid calculations

TABLE NO. 1 TABLE ITEM: %RH ROW ITEM DRYB COL. ITEM WETB

Column Values: 70 68 66

Row No.	Row Value	Table Values		
		70	68	66
1	80	63	56	50
2	85	49	44	39
3	90	39	34	30

TABLE NO. 2 TABLE ITEM: DEWP ROW ITEM DRYB COL. ITEM WETB

Column Values: 70 68 66

Row No.	Row Value	Table Values		
		70	68	66
1	80	66	63	60
2	85	64	61	57
3	90	62	58	54

Exhibit 11.—RH run obtaining tables of humidity and dew point.

OPERATING THE MODULES IN "LINKED" RUNS

"Linked" runs provide the capability to use results from one program module in another program module. Level 2 or 3 modules may be linked to specific level 1 or 2 modules, respectively, as shown in figure 1. Thus SIZE, SCORCH, MAP, and TWO may be linked to DIRECT, while MAP and CONTAIN may be linked to SIZE. MAP may also be linked to SIZE or SPOT when they are run independently.

Remember that multiple values may be entered for a maximum of two input items, including those passed from a linked module. Depending on the number of items for which multiple values are entered, you may pass to the "linked" module:

- a single value for each output item—one value entered for each input item,
- a list of values for each output item—two or three values entered for one input item,
- a table of values for each output item—two or three values entered for each of two input items.

If a set of single output values is passed forward, a list can be produced from the linked module by entering two or three values for **one** of the linked module inputs. A table would be produced by the linked module if multiple values were entered for **two** of the linked module inputs. If a list is passed forward to a linked module, a table may be produced by entering two or three values for one linked module input. If a table is passed forward, multiple values may **not** be entered for **any** linked module input.

Output produced by running a module independently will not be passed to another module that is also run independently. For example, if you run the DIRECT module from the MAIN program, then also run the SIZE module from MAIN after quitting DIRECT; the outputs from DIRECT will **not** be passed to SIZE. This would have to be accomplished by first running DIRECT, then selecting the SIZE module while you are still in the DIRECT module. SIZE output could similarly be passed to MAP or CONTAIN by selecting one of these modules while still in the SIZE module. In addition, you can link to another module only after a successful run using the module you are currently in. Otherwise, the display will briefly show the error message, "NO LINK BEFORE RUN". If any inputs are changed, a new run is necessary.

Linked run forms were considered, but found to be complicated and numerous if they were to be made for all possible combinations. Use the forms for individual modules. If multiple values are entered for one input item, the linked module will list the multiple output values. If a table is passed from one module to the next, then listing the inputs in the linked module will display the range of table values passed. The form of the display is: "ITEM LABEL value TO value". For example, "AREA 65 TO 303". Use the space provided for multiple inputs of this item to write this range on the data sheet for the linked module.

Linked DIRECT-SIZE-CONTAIN Run

An example DIRECT-SIZE-CONTAIN run is shown in exhibits 12a, 12b, and 12c. The rate of spread and effective windspeed, in the direction of maximum spread rate, are passed to SIZE. ROS and EWS passed to SIZE or CONTAIN are always in the direction of maximum spread rate. The ROS and EWS in the output list of DIRECT can be in other directions if that option was selected for input item 10 (SDIR) of DIRECT. Thus, outputs from linked SIZE or CONTAIN runs are independent of the spread direction input in DIRECT. The output from DIRECT is a list of three values for each output item. This is expanded to tabular output by entering three elapsed time (ET) values in SIZE, shown in exhibit 12b. Only single values can be entered in CONTAIN (exhibit 12c) because tables of AREA and L/W were passed to it from SIZE. That is, only one total line-building rate (TLBR) could be entered.

The AREA table produced by SIZE in exhibit 12b shows the size of the fire (acres) if it were to burn unconstrained for the nine combinations of three 1-hour fuel moistures (10, 11, and 12 percent) and three time intervals (1.0, 1.5, and 2.0 hours). These areas become the initial fire area for CONTAIN in exhibit 12c. Note that the SIZE module prompt "SIZE: I,L,R,MA,CO,Q" now gives you the option to go to CONTAIN. This option is only available in linked runs and not available in independent runs.

The final fire size (FFS) table produced by CONTAIN in exhibit 12c shows the size of the fire (acres) for the same nine combinations of 1-hour fuel moisture and burning time, but with suppression action being taken by forces attacking the fire from the rear. These forces have a total line construction rate capability of 100 chains per hour. The TIME table of CONTAIN shows how long it will take to contain the fire at the sizes listed in the FFS table.

DIRECT MODULE (English Units)

LIST NUMBER 37a

(Keywords: Input, List, Run, Quit, SIze, SCorch, MAp, TWo)

INPUT	(Input, List)					
1	MODEL #	Fuel model number	(1-99)		3	
2	1H	1-H fuel moisture	[1-60%]	10.0	11.0	12.0
3	10H	[1]10-H fuel moisture	[1-60%]	—		
4	100H	[1]100-H fuel moisture	[1-60%]	—		
5	HERB	[1]Live herb moisture	[30-300%]	—		
6	WOOD	[1]Live woody moisture	[30-300%]	—		
7	MFWS	Midflame windspeed	[0-99 mi/h]	2		
8	SLP	Slope	[0-100%/ 0-45 degrees]	20%		
9	WDIR	[2]Direction of wind vector, deg. clockwise from uphill	[0-360 degrees]	0		
	PREDICT AT MAX		(Y/N)		Y	
10	SDIR	Direction of spread calc., deg. clockwise from uphill (or from wind vector if slope is zero)	[0-360 degrees]			MAX
OUTPUT	(Run)					
0		No more tables				
1	ROS	Rate of spread	ch/h	35	34	32
2	H/A	Heat per unit area	Btu/ft^2	662	654	648
3	FLI	Fireline intensity	Btu/ft/s	427	404	385
4	FL	Flame length	ft	7.3	7.1	7.0
5	RI	Reaction intensity	Btu/ft^2/min	2,585	2,555	2,53
6	EWS	Effective windspeed in direction SDIR	mi/h	2.3	2.3	2.3
7	MAXD	[3]Direction of maximum spread, deg. clockwise from uphill	degrees	0	0	0

[1]Input only if corresponding fuel load is not zero.
[2]Input only if midflame windspeed (MFWS) and slope (SLP) are not zero.
[3]Output only if calculations are in direction of maximum spread.

Exhibit 12a.—DIRECT run obtaining outputs that can be linked to SIZE.

SIZE MODULE (English Units)

LIST NUMBER 37b

(Keywords: Input, List, Run, MAp, [1]COntain, Quit)

INPUT	(Input, List)					
1	ROS	[2]Rate of spread	[0.1-500 ch/h]	35	34	32
2	EWS	[2]Effective windspeed	[0-99 mi/h]	2.3	2.3	2.3
3	ET	Elapsed time	[0.1 - 8 h]	1.0	1.5	2.0
OUTPUT	(Run)					
0		No more tables				
1	AREA	Area	acres	see output table on next page.		
2	PER	Perimeter	ch			
3	L/W	Length-to-width ratio				
4	FSD	Forward spread distance	ch			
5	BSD	Backing spread distance	ch			
6	MXW	Maximum fire width	ch			

[1]SIZE can link to CONTAIN only if linked to DIRECT.
[2]Input only when SIZE is used as an independent module.

Exhibit 12b.—Linked SIZE run using DIRECT outputs shown in exhibit 12a.

OUTPUT TABLES

LIST NUMBER 37b

TABLE NO. 1 TABLE ITEM: AREA ROW ITEM IH COL. ITEM ET

Row No.	Row Value	Column Values: 1.0	1.5	2.0
		Table Values		
1	10.0	79	177	316
2	11.0	73	163	290
3	12.0	67	151	268

TABLE NO. 2 TABLE ITEM: PER ROW ITEM IH COL. ITEM ET

Row No.	Row Value	Column Values: 1.0	1.5	2.0
		Table Values		
1	10.0	103	155	207
2	11.0	99	149	198
3	12.0	95	143	191

TABLE NO. 3 TABLE ITEM: L/W ROW ITEM IH COL. ITEM ET

Row No.	Row Value	Column Values: 1.0	1.5	2.0
		Table Values		
1	10.0	1.6	1.6	1.6
2	11.0	1.6	1.6	1.6
3	12.0	1.6	1.6	1.6

Exhibit 12b. (Con.)

CONTAIN MODULE (English Units)

LIST NUMBER 37c

(Keywords: Input, List, Run, Quit)

INPUT	(Input, List)					
1	RUN OPT	Run option 1 = calculate total line building rate 2 = calculate burned area	(1 or 2)		2	
2	ATTACK OPT	Attack option 1 = head 2 = rear	(1 or 2)		2	
3	ROS	[1]Rate of spread	[0.1-500 ch/h]	35	34	32
4	AREA	[1]Initial fire area	[0.1-100 acres]	67	to	316
5	L/W	[1]Length-to-width ratio	[1-5]	1.6	to	1.6
6	BAT	[2]Burned area target	[0.1-2000 acres]	—		
7	TLBR	[3]Total line building rate	[0.1-800 ch/h]	100.0		
OUTPUT	(Run)			See output tables on next page.		
1	PER	Total length of line	chains			
2	TIME	Containment time	hours			
3	FFS	[4]Final fire size	acres			
3	TLBR	[5]Total line building rate	ch/h			
4	MAXA	[5]Maximum area calculable	acres			
5	MINA	[5]Minimum area calculable	acres			

Error Codes:

−1 = Burned area target too large, cannot calculate slow enough line building rate
−2 = Line building rate too slow to catch fire
−3 = L/W ratio too large
−4 = Burned area target too close to initial fire size
−5 = Line building rate too fast

[1]Input only when CONTAIN is used as an independent module.
[2]Input only for run option = 1 (calculate total line building rate).
[3]Input only for run option = 2 (calculate burned area target).
[4]Output only for run option = 2.
[5]Output only for run option = 1.

Exhibit 12c.—Linked CONTAIN run using outputs from DIRECT and SIZE.

OUTPUT TABLES

LIST NUMBER 37c

TABLE NO. 1 TABLE ITEM: PER ROW ITEM IH COL. ITEM ET

Row No.	Row Value	Column Values: 1.0	1.5	2.0
		Table Values		
1	10.0	385	578	771
2	11.0	334	501	668
3	12.0	296	444	592

TABLE NO. 2 TABLE ITEM: TIME ROW ITEM IH COL. ITEM ET

Row No.	Row Value	Column Values: 1.0	1.5	2.0
		Table Values		
1	10.0	3.9	5.8	7.7
2	11.0	3.3	5.0	6.7
3	12.0	3.0	4.4	5.9

TABLE NO. 3 TABLE ITEM: FFS ROW ITEM IH COL. ITEM ET

Row No.	Row Value	Column Values: 1.0	1.5	2.0
		Table Values		
1	10.0	773	1,740	3,093
2	11.0	600	1,351	2,402
3	12.0	484	1,090	1,937

Exhibit 12c. (Con.)

SCORCH MODULE (English Units)

(Keywords: Input, List, Run, Quit)

INPUT (Input, List)

1	TEMP	Ambient air temperature	[33-120 °F]	80		
2	FL	[1]Flame length	[0.1-20 ft]	7.3	7.1	7.0
3	MFWS	[1]Midflame windspeed	[0-10 mi/h]	2		

OUTPUT (Run)

1	SCHT	Scorch height	feet	59	57	55

[1]Input only if SCORCH is used as an independent module.

TABLE NO. 1 TABLE ITEM: Scorch height ROW ITEM ______ COL. ITEM ______

Column Values: ______ ______ ______

Row No.	Row Value	Table Values		
1				
2				
3				

Exhibit 13.—Linked SCORCH run obtaining a list of scorch heights from the DIRECT outputs of exhibit 12a.

Linked DIRECT-SCORCH Run

The DIRECT run in the previous example (exhibit 12a) can be linked to SCORCH by entering SC after a valid DIRECT run. The midflame windspeed and flame length in the direction of spread selected by SDIR are passed to SCORCH. Only air temperature needs to be input for SCORCH calculations. The calculations are not corrected for slope; erroneous results may be obtained for slopes steeper than 30 percent. The output of SCORCH linked to DIRECT is shown in exhibit 13.

Linked DIRECT-TWO Run

The TWO module is available only by linking to it through DIRECT. This module is used to weight the spread rate of fire through two very different fuel types that occur as interspersed patches in the same general area.

First, run DIRECT with the fuel model and environmental conditions that describe the situation for one of the vegetation types. Then do a second run for the other fuel model. Except for model number, all other DIRECT inputs common to both models should be equal for both runs. If the second model requires additional moisture inputs for additional fuel classes, these inputs should be made. DIRECT must produce single output, list output, or tabular output for **both** models. That is, you cannot link to TWO if you have, for example, produced a list output with the first model and a tabular output with the second. This will produce the message "INPUT ERROR".

After doing both DIRECT runs, enter keyword TW to link to the TWO module. A List at this point will produce a list of five items, the first four of which were values passed to TWO by DIRECT. Items 1 and 2 (MODEL1 and MODEL2, respectively) display the numbers of the fuel models used in the first and second DIRECT runs. Items 3 and 4 list the spread rates produced by the first and second models run by DIRECT. Spread rates are for the direction selected for the calculation in input item 10 (SDIR) of DIRECT.

The spread rates will be presented as single values, lists, or a range of values, depending on how many DIRECT input items were assigned multiple values. All of TWO items 1-4 are passed by DIRECT; you cannot enter any of them independently. You must, however, enter values for input item 5 — COV1. This is the percentage of area covered by the first fuel model run in DIRECT (item MODEL1). No input is needed for area coverage of the second model, as it is assumed to cover the remainder of the area.

The rate of spread calculated by TWO is not passed back to DIRECT, nor can it be used in SIZE or CONTAIN calculations. Once a Run is made in TWO, a

return to DIRECT will not allow subsequent links to other modules until a valid DIRECT Run is made.

An example follows in which two fuel models are run in DIRECT to produce two lists of spread rates (exhibits 14a and 14b). After the second Run a link is made to TWO as shown in exhibit 14c. Both fuel model numbers and the ROS output from DIRECT are passed to TWO. Only input 5, the area coverage (percent) of the first model (COV1), is needed to complete the input list in TWO. Three percentages of coverage were entered and a table of weighted ROS is output, as shown in the TWO data sheet.

DIRECT MODULE (English Units)

LIST NUMBER 40a

(Keywords: Input, List, Run, Quit, SIze, SCorch, MAp, TWo)

INPUT	(Input, List)					
1	MODEL #	Fuel model number	(1-99)		1	
2	1H	1-H fuel moisture	[1-60%]	8.0	10.0	12.0
3	10H	[1]10-H fuel moisture	[1-60%]	–		
4	100H	[1]100-H fuel moisture	[1-60%]	–		
5	HERB	[1]Live herb moisture	[30-300%]	–		
6	WOOD	[1]Live woody moisture	[30-300%]	–		
7	MFWS	Midflame windspeed	[0-99 mi/h]	4		
8	SLP	Slope	[0-100%/ 0-45 degrees]	20%		
9	WDIR	[2]Direction of wind vector, deg. clockwise from uphill	[0-360 degrees]	0		
	PREDICT AT MAX		(Y/N)		Y	
10	SDIR	Direction of spread calc., deg. clockwise from uphill (or from wind vector if slope is zero)	[0-360 degrees]			MAX
OUTPUT	(Run)					
0		No more tables				
1	ROS	Rate of spread	ch/h	58	39	0
2	H/A	Heat per unit area	Btu/ft^2	84	59	0
3	FLI	Fireline intensity	Btu/ft/s	90	42	0
4	FL	Flame length	ft	3.6	2.5	0
5	RI	Reaction intensity	Btu/ft^2/min	764	538	0
6	EWS	Effective windspeed in direction SDIR	mi/h	4.2	4.2	0
7	MAXD	[3]Direction of maximum spread, deg. clockwise from uphill	degrees	0	0	0

[1]Input only if corresponding fuel load is not zero.
[2]Input only if midflame windspeed (MFWS) and slope (SLP) are not zero.
[3]Output only if calculations are in direction of maximum spread.

Exhibit 14a.—First DIRECT run for linking to TWO in exhibit 14c.

DIRECT MODULE (English Units)

LIST NUMBER ____________

(Keywords: Input, List, Run, Quit, SIze, SCorch, MAp, TWo)

INPUT	(Input, List)					
1	MODEL #	Fuel model number	(1-99)		4	
2	1H	1-H fuel moisture	[1-60%]	8.0	10.0	12.0
3	10H	[1]10-H fuel moisture	[1-60%]	10.0		
4	100H	[1]100-H fuel moisture	[1-60%]	12.0		
5	HERB	[1]Live herb moisture	[30-300%]	–		
6	WOOD	[1]Live woody moisture	[30-300%]	90		
7	MFWS	Midflame windspeed	[0-99 mi/h]	4		
8	SLP	Slope	[0-100%/ 0-45 degrees]	20		
9	WDIR	[2]Direction of wind vector, deg. clockwise from uphill	[0-360 degrees]	0		
	PREDICT AT MAX		(Y/N)		Y	
10	SDIR	Direction of spread calc., deg. clockwise from uphill (or from wind vector if slope is zero)	[0-360 degrees]			MAX
OUTPUT	(Run)					
0		No more tables				
1	ROS	Rate of spread	ch/h	61	59	56
2	H/A	Heat per unit area	Btu/ft^2	2,527	2,467	2,405
3	FLI	Fireline intensity	Btu/ft/s	2,846	2,667	2,490
4	FL	Flame length	ft	17.5	17.0	16.4
5	RI	Reaction intensity	Btu/ft^2/min	11,445	11,175	10,893
6	EWS	Effective windspeed in direction SDIR	mi/h	4.2	4.2	4.2
7	MAXD	[3]Direction of maximum spread, deg. clockwise from uphill	degrees	0	0	0

[1]Input only if corresponding fuel load is not zero.
[2]Input only if midflame windspeed (MFWS) and slope (SLP) are not zero.
[3]Output only if calculations are in direction of maximum spread.

Exhibit 14b.—Second DIRECT run for linking to TWO in exhibit 14c.

TWO MODULE (English Units)

(Keywords: Input, List, Run, Quit)

PASSED FROM DIRECT (List)

1	MODEL1	First model run by DIRECT			1	
2	MODEL2	Second model run by DIRECT			4	
3	ROS1	Spread rate for first model		58	39	0
4	ROS2	Spread rate for second model		61	59	56

INPUT (Input, List)

5	COV1	Percent area coverage first model	[20-80%]	30	50	70

OUTPUT (Run)

1	ROS	Rate of spread	ch/h			

TABLE NO. 1 TABLE ITEM: Weighted ROS ROW ITEM 1H COL. ITEM COV1

Row No.	Row Value	Column Values: 30	50	70
		Table Values		
1	8.0	61	60	59
2	10.0	53	49	45
3	12.0	40	28	17

Exhibit 14c.—Linked TWO run using spread rates calculated for two models in exhibits 14a and 14b.

Linked MAP Runs

Linking to MAP from SIZE, SPOT, and DIRECT results in automatic selection of the MAP units option 1, 2, and 3, respectively. SIZE passes three distances to MAP—forward spread distance, backing spread distance, and maximum fire width. These three distances change the input item names on the independent MAP input sheets, and result in the three output map distances. SPOT passes a maximum spotting distance in miles. DIRECT passes a rate of spread to MAP where spread time is needed for MAP to calculate forward spread distance. Exhibits 15, 16, and 17 show examples of these different linked runs. A printer was used as a list device, but if no printer is attached, the same output can be seen on the display by stepping through the lists.

```
1  ROS    40.0    60.0    80.0
2  EWS     5.0                    SIZE   List
3  ET      2.0
=============================
   ROS    40.0    60.0    80.0
=============================
1  AREA   249     559     995
2  PER    199     298     397     SIZE   Run
3  L/W     2.3     2.3     2.3
4  FSD    80.0   120.0   160.0
5  BSD     4.4     6.6     8.8
6  MXW    37.5    56.3    75.0
=============================

1  SCL OPT                2
3  IN/MI                  1.000
4  UNITS OPT              1
5  FSD    80.0   120.0   160.0    MAP    List
6  BSD     4.4     6.6     8.8
7  MXW    37.5    56.3    75.0
=============================
   ROS    40.0    60.0    80.0
=============================
1  MFSD    1.0     1.5     2.0    MAP    Run
2  MBSD    0.0     0.0     0.1
3  MMXW    0.5     0.7     0.9
=============================
```

Exhibit 15.—Example of SIZE run followed by link to MAP.

```
 1  BRAND SRC          1
 2  MCHT 100
 3  20'W 10      15       20
 4  RVEL 1000
 5  RVHD 1.0                     SPOT   List
 6  SRC LOC            1
 7  TREE SP            1
 8  DBH   20
 9  TRHT  80
10  #TR   10
=============================
    20'W  10     15       20
=============================     SPOT   Run
 1  SPOT  0.26   0.39     0.53
=============================

 1  SCL OPT               2
 3  IN/MI                 2.000
 4  UNITS OPT             2       MAP    List
 6  SPOT  0.26   0.39     0.53
=============================
    20'W  10     15       20
=============================     MAP    Run
 1  MSPT  0.51   0.78     1.05
=============================
```

Exhibit 16.—Example of SPOT run followed by link to MAP.

```
 1     MODEL #           2
 2     1H        8.0
 3     10H      10.0
 4     100H     12.0
 5     HERB     80
 7     MFWS      5       7       10            DIRECT  List
 8     SLP      10
 9     WDIR     90
10     SDIR                    MAX
=========================
       MFWS     5       7       10
=========================
 1     ROS     35      62      118
 2     H/A    463     463      463             DIRECT  Run
 3     FLI    294     529      999
 4     FL     6.2     8.1     10.8
 5     RI    3357    3357     3357
 6     EWS    5.0     7.0     10.0
 7     MAXD  89      89       90
=========================

 1     SCL  OPT          2
 3     IN/MI             1.000
 4     UNITS  OPT        3                     MAP     List
 7     ROS    35      62      118
 8     TIME   2.0
=========================
       MFWS  5       7       10
=========================                      MAP     Run
 1     MFSD  0.9     1.6     2.9
=========================
```

Exhibit 17.—Example of DIRECT run followed by link to MAP.

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APPENDIX A: DATA SHEETS, ENGLISH UNITS OF MEASURE

FUEL MODEL MODULE (English Units)

(Keywords: Get, Input, List, Save, Quit, List Models, Delete Models)

INPUT LIST (Input, List)

1	MODEL #	Fuel model number	(14 - 99)	________
2	NAME	Fuel model name	(22 char. max.)	________
3	1HR LOAD	1-hour load	(0.01-30 tons/acre)	________
4	10HR LOAD	10-hour load	(0-30 tons/acre)	________
5	100HR LOAD	100-hour load	(0-30 tons/acre)	________
6	HERB LOAD	Live herb load	(0-30 tons/acre)	________
7	WOOD LOAD	Live woody load	(0-30 tons/acre)	________
8	1HR S/V	1-hour surface/volume ratio	(1,200-3,500 ft^2/ft^3)	________
9	HERB S/V	[1]Herb surface/volume ratio	(1,200-3,500 ft^2/ft^3)	________
10	WOOD S/V	[2]Woody surface/volume ratio	(1,200-3,500 ft^2/ft^3)	________
11	DEPTH	Fuel bed depth	(0.1 - 10 ft)	________
12	HEAT	Fuel heat content	(7,000-12,000 Btu/lb)	________
13	MOIS EXT	Dead fuel extinction moisture	(10 - 50%)	________
14	STATIC-DYNAM	Static or dynamic model 0 = static or herb load is zero 1 = dynamic	(0 or 1)	________
15	WIND FACTOR	Exposed fuel wind adjustment factor	(0.01 - 1)	________

[1]Input only if herb load is greater than zero.
[2]Input only if wood load is greater than zero.

USER FUEL MODEL FILE CONTENTS (List Models)

Model Number	Model Name (22 characters maximum)

DIRECT MODULE (English Units)

LIST NUMBER ________

(Keywords: Input, List, Run, Quit, SIze, SCorch, MAp, TWo)

INPUT	(Input, List)					
1	MODEL #	Fuel model number	(1-99)		____	
2	1H	1-H fuel moisture	[1-60%]	____	____	____
3	10H	[1]10-H fuel moisture	[1-60%]	____	____	____
4	100H	[1]100-H fuel moisture	[1-60%]	____	____	____
5	HERB	[1]Live herb moisture	[30-300%]	____	____	____
6	WOOD	[1]Live woody moisture	[30-300%]	____	____	____
7	MFWS	Midflame windspeed	[0-99 mi/h]	____	____	____
8	SLP	Slope	[0-100% or 0-45 degrees]	____	____	____
9	WDIR	[2]Direction of wind vector, deg. clockwise from uphill	[0-360 degrees]	____	____	____
	PREDICT AT MAX		(Y/N)		____	
10	SDIR	Direction of spread calc., deg. clockwise from uphill (or from wind vector if slope is zero)	[0-360 degrees]	____	____	____
OUTPUT	(Run)					
0		No more tables				
1	ROS	Rate of spread	ch/h	____	____	____
2	H/A	Heat per unit area	Btu/ft^2	____	____	____
3	FLI	Fireline intensity	Btu/ft/s	____	____	____
4	FL	Flame length	ft	____	____	____
5	RI	Reaction intensity	Btu/ft^2/min	____	____	____
6	EWS	Effective windspeed in direction SDIR	mi/h	____	____	____
7	MAXD	[3]Direction of maximum spread, deg. clockwise from uphill	degrees	____	____	____

[1]Input only if corresponding fuel load is not zero.
[2]Input only if midflame windspeed (MFWS) and slope (SLP) are not zero.
[3]Output only if calculations are in direction of maximum spread.

SIZE MODULE (English Units)

LIST NUMBER ____________

(Keywords: Input, List, Run, MAp, [1]COntain, Quit)

INPUT (Input, List)

1	ROS	[2]Rate of spread	[0.1-500 ch/h]	____	____	____
2	EWS	[2]Effective windspeed	[0-99 mi/h]	____	____	____
3	ET	Elapsed time	[0.1 - 8 h]	____	____	____

OUTPUT (Run)

0		No more tables				
1	AREA	Area	acres	____	____	____
2	PER	Perimeter	ch	____	____	____
3	L/W	Length-to-width ratio		____	____	____
4	FSD	Forward spread distance	ch	____	____	____
5	BSD	Backing spread distance	ch	____	____	____
6	MXW	Maximum fire width	ch	____	____	____

[1]SIZE can link to CONTAIN only if linked to DIRECT.
[2]Input only when SIZE is used as an independent module.

CONTAIN MODULE (English Units)

LIST NUMBER ____________

(Keywords: Input, List, Run, Quit)

INPUT (Input, List)

1	RUN OPT	Run option 1 = calculate total line building rate 2 = calculate burned area	(1 or 2)		____	
2	ATTACK OPT	Attack option 1 = head 2 = rear	(1 or 2)		____	
3	ROS	[1]Rate of spread	[0.1-500 ch/h]	____	____	____
4	AREA	[1]Initial fire area	[0.1-100 acres]	____	____	____
5	L/W	[1]Length-to-width ratio	[1-5]	____	____	____
6	BAT	[2]Burned area target	[0.1-2000 acres]	____	____	____
7	TLBR	[3]Total line building rate	[0.1-800 ch/h]	____	____	____

OUTPUT (Run)

1	PER	Total length of line	chains	____	____	____
2	TIME	Containment time	hours	____	____	____
3	FFS	[4]Final fire size	acres	____	____	____
3	TLBR	[5]Total line building rate	ch/h	____	____	____
4	MAXA	[5]Maximum area calculable	acres	____	____	____
5	MINA	[5]Minimum area calculable	acres	____	____	____

Error Codes:

-1 = Burned area target too large, cannot calculate slow enough line building rate
-2 = Line building rate too slow to catch fire
-3 = L/W ratio too large
-4 = Burned area target too close to initial fire size
-5 = Line building rate too fast

[1]Input only when CONTAIN is used as an independent module.
[2]Input only for run option = 1 (calculate total line building rate).
[3]Input only for run option = 2 (calculate burned area target).
[4]Output only for run option = 2.
[5]Output only for run option = 1.

SPOT MODULE (English Units)

LIST NUMBER ________

(Keywords: Input, List, Run, MAp, Quit)

INPUT (Input, List)

1	BRAND SRC	Firebrand source 1 = torching trees 2 = burning piles 3 = wind-driven surface fire	(1-3)		____	
2	MCHT	Mean cover height	[0-300 ft]	____	____	____
3	20'W	20-ft windspeed	[0-99 mi/h]	____	____	____
4	RVEL	Ridge-to-valley elevation difference	[0-4,000 ft]	____	____	____
5	RVHD	Ridge-to-valley horiz. distance	[0-4 mi]	____	____	____
6	SRC LOC	Spotting source location 0 = midslope, windward side 1 = valley bottom 2 = midslope, leeward side 3 = ridgetop	(0-3)		____	
7	TREE SP	[1]Tree species 1 = Engelmann spruce 2 = Douglas-fir, subalpine fir 3 = hemlock 4 = ponderosa, lodgepole pine 5 = white pine 6 = balsam fir, grand fir	(1-6)		____	
8	DBH	[1]Torching tree DBH	[5-40 inches]	____	____	____
9	TRHT	[1]Torching tree height	[10-300 ft]	____	____	____
10	#TR	[1]Number of torching trees	[1-30]	____	____	____
11	FLHT	[2]Continuous flame height	[1-100 ft]	____	____	____
12	FL	[3]Flame length	[0.1-50 ft]	____	____	____
13	MODEL #	[3]Fuel model	(1-99)		____	
14	HERB	[4]Herbaceous moisture	[30-300%]	____	____	____

OUTPUT (Run)

1	SPOT	Maximum spotting distance	mi	____	____	____

[1]Input only for firebrand source = 1 (torching tree option).
[2]Input only for firebrand source = 2 (burning pile option).
[3]Input only for firebrand source = 3 (wind-driven surface fire option).
[4]Input only for dynamic fuel models with a herbaceous fuel load.

SCORCH MODULE (English Units)

(Keywords: Input, List, Run, Quit)

INPUT (Input, List)

1	TEMP	Ambient air temperature	[33-120 °F]	____	____	____
2	FL	[1]Flame length	[0.1-20 ft]	____	____	____
3	MFWS	[1]Midflame windspeed	[0-10 mi/h]	____	____	____

OUTPUT (Run)

1	SCHT	Scorch height	feet	____	____	____

[1]Input only if SCORCH is used as an independent module.

TABLE NO. 1 TABLE ITEM: Scorch height ROW ITEM ____ COL. ITEM ____

Column Values: ____ ____ ____

Row No.	Row Value	Table Values		
1	____	____	____	____
2	____	____	____	____
3	____	____	____	____

IGNITE MODULE (English Units)

(Keywords: Input, List, Run, Quit)

INPUT (Input, List)

1	TEMP	Ambient air temperature	[33-120 °F]	______	______	______
2	1H	1-h fuel moisture	[1-60%]	______	______	______
3	SHAD	Shade	[0-100%]	______	______	______

OUTPUT (Run)

1	P(I)	Probability of ignition	pct	______	______	______

TABLE NO. 1 TABLE ITEM: Prob. of Ignition ROW ITEM ______ COL. ITEM ______

Column Values: ______ ______ ______

Row No.	Row Value	Table Values		
1	______	______	______	______
2	______	______	______	______
3	______	______	______	______

MOISTURE MODULE (English Units)

LIST NUMBER ____________

(Keywords: Input, List, Run, Quit)

INPUT (Input, List)

1	RUN OPT	Run option 1 = Burn time calculations 2 = Hourly calculations	(1 or 2)		______	

TIME AND LOCATION

2	BURN MONTH	Month of burn	(1-12)		______	
3	BURN DAY	Day of burn	(1-31)		______	
4	LATITUDE	Latitude of fire location	(−90 to 90 degrees)		______	
5	BURN TIME	Time of burn	(0-2,359 h)		______	

FUEL MODEL

6	MODEL #	Fuel model number	(1-99)		______	

SLOPE, ELEVATION, ASPECT

11	SLP	Slope steepness	[0-100% or 0-45 degrees]	______	______	______
12	ELFL	Elevation of fire location	[0-12,000 ft]	______	______	______
	RH OBS AT FIRE		(Y/N)		______	
13	ELOB	Elevation of T&RH observations	(0-12,000 ft)		______	
14	ASPECT	Aspect of fire location 0 = north 180 = south 90 = east 270 = west	(0-360 degrees)		______	

TIMBER OVERSTORY DESCRIPTION

15	CCLO	Crown closure	[0-100%]	______	______	______
16	FOLIAGE	Foliage presence 0 = absent 1 = present	(0 or 1)		______	
17	SHADE TOL	Shade tolerance 0 = intolerant 1 = tolerant	(0 or 1)		______	
18	DOM TYPE	Dominant tree type 1 = coniferous 2 = deciduous	(1 or 2)		______	
19	AVHT	Average tree height	[10-300 ft]	______	______	______
20	H/H	Crown height/tree height ratio	[0.1-1]	______	______	______
21	H/D	Crown height/crown diameter ratio	[0.2-5]	______	______	______

MOISTURE MODULE (continued, English Units)

LIST NUMBER ______

EARLY AFTERNOON WEATHER

22	14T	Burn day 1400 temperature	[33-120 °F]	______	______	______
23	14RH	Burn day 1400 relative humidity	[1-100%]	______	______	______
24	14W	Burn day 1400 20-ft windspeed	[0-99 mi/h]	______	______	______
25	14CC	Burn day cloud cover	[0-100%]	______	______	______
26	14HZ	Burn day 1400 haziness	[1-4]	______	______	______

1 = very clear sky
2 = average clear forest atmosphere
3 = moderate blue haze
4 = dense haze—moderate smoke

SUNSET WEATHER

27	SST	Sunset temperature	[33-120 °F]	______	______	______
28	SSRH	Sunset relative numidity	[1-100%]	______	______	______
29	SSW	Sunset 20-ft windspeed	[0-99 mi/h]	______	______	______
30	SSCC	Sunset cloud cover	[0-100%]	______	______	______

SUNRISE WEATHER

31	SRT	Sunrise temperature	[33-120 °F]	______	______	______
32	SRRH	Sunrise relative humidity	[1-100%]	______	______	______
33	SRW	Sunrise 20-ft windspeed	[0-99 mi/h]	______	______	______
34	SRCC	Sunrise cloud cover	[0-100%]	______	______	______

BURN TIME WEATHER

35	BTT	Burn time temperature	[33-120 °F]	______	______	______
36	BTRH	Burn time relative humidity	[1-100%]	______	______	______
37	BTW	Burn time 20-ft windspeed	[0-99 mi/h]	______	______	______
38	BTCC	Burn time cloud cover	[0-100%]	______	______	______
39	BTHZ	Burn time haziness	[1-4]	______	______	______

1 = very clear sky
2 = average clear forest atmosphere
3 = moderate blue haze
4 = dense haze—moderate smoke

MOISTURE MODULE (continued, English Units)

LIST NUMBER ____________

JRN TIME WIND

40	EXPOSURE	Exposure of fuels to wind 1 = exposed 2 = partially sheltered 3 = fully sheltered—open stand 4 = fully sheltered—dense stand 5 = direct entry of wind adjustment factor	(1-5)	______
41	WAF	Wind adjustment factor Exposure 5 only	(0-1)	______

OISTURE INITIALIZATION OPTION

43	MOIS OPT	Moisture initialization option 1 = fine fuel moisture known for day before burn 2 = not allowed 3 = incomplete data; rain the week before burn 4 = incomplete data; no rain the week before burn 5 = incomplete data; weather pattern changing	(1-5)	______

OISTURE OPTION 1

44	FM-1	Burn day −1 fine fuel moisture	[1-100%]	______	______	______

OISTURE OPTION 3

51	RDAY	Number of days before burn that rain occurred	[1-7 days]	______	______	______
52	RAIN	Rain amount, hundredths of an inch	[0-400]	______	______	______
53	RDT	1400 temperature on rain day	[33-120 °F]	______	______	______
54	SKY CODE	Sky condition from rain day to burn day 1 = clear 2 = cloudy 3 = partly cloudy	(1-3)		______	

OISTURE OPTION 4

No additional input.

MOISTURE MODULE (continued, English Units)

LIST NUMBER ______

MOISTURE OPTION 5

55	TD-1	Burn day −1 1400 temperature	[33-120 °F]	______	______	______
56	RD-1	Burn day −1 1400 relative humidity	[1-100%]	______	______	______
57	WD-1	Burn day −1 1400 20-ft windspeed	[0-99 mi/h]	______	______	______
58	CD-1	Burn day −1 1400 cloud cover	[0-100%]	______	______	______
59	WTHR	Weather condition prior to burn day −1 1 = hot and dry 2 = cool and wet 3 = between 1 and 2	[1-3]	______	______	______

OUTPUT (Run)

1	MOIS	1-hour fuel moisture	pct	______	______	______
2	TEMP	Fuel level temperature	°F	______	______	______
3	%RH	Fuel level relative humidity	pct	______	______	______
4	SHAD	Percent of area shaded	pct	______	______	______
5	P(I)	Probability of ignition	pct	______	______	______

MOISTURE MODULE (continued, English Units)

LIST NUMBER ____________

OURLY OUTPUT (Run)

TIME	FMOIST pct	FTEMP °F	FRH pct
14			
15			
16			
17			
18			
19			
20			
21			
22			
23			
24			
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			
11			
urn Time ______			

MAP MODULE (English Units)

LIST NUMBER ______

(Keywords: Input, List, Run, Quit)

INPUT (Input, List)

1	SCL OPT	Scale option 1 = Representative fraction 2 = Inches per mile	(1 or 2)			
2	RF/1000	[1]Representative fraction/1,000 e.g., RF of 1/24,000 = 24	(1-500)			
3	IN/MI	[2]Inches per mile	(0.0625-8)			
4	UNITS OPT	Units option 1 = Spread distance 2 = Spot distance 3 = Rate of spread	(1-3)			
5	DIST	[3]Spread distance	[0-1000 ch]			
6	SPOT	[4]Spot distance	[0.1-10 mi]			
7	ROS	[5]Rate of spread	[0.1-500 ch/h]			
8	TIME	[5]Elapsed time	[0.1-8 h]			
5	FSD	[6]Forward spread distance	ch			
6	BSD	[6]Backing spread distance	ch			
7	MXW	[6]Maximum fire width	ch			

OUTPUT (Run)

1	MFSD	Forward spread distance on map (UNITS OPT = 1 or 3)	inches			
1	MSPT	Forward spot distance on map (UNITS OPT = 2)	inches			
2	MBSD	Backing spread distance on map (SIZE linked only)	inches			
3	MMXW	Maximum fire width on map (SIZE linked only)	inches			

[1]Input only for scale option = 1.
[2]Input only for scale option = 2.
[3]Input only for units option = 1.
[4]Input only for units option = 2.
[5]Input only for units option = 3.
[6]Passed from SIZE for linked run only. No input is needed.

SLOPE MODULE (English Units)

LIST NUMBER ____________

(Keywords: Input, List, Run, Quit)

From Point _____ to Point _____

NPUT (Input, List)

1	SCL OPT	Scale option 1 = Representative fraction 2 = Inches per mile	(1 or 2)	______
2	RF/1000	[1]Representative fraction/1,000 e.g., RF of 1/24,000 = 24	(1-500)	______
3	IN/MI	[2]Inches per mile	(0.0625-8)	______
4	CON INT	Contour interval	(10-500 ft)	______
5	MAP DIST	Map distance	(0.1-10 in)	______
6	# INTVLS	Number of contour intervals	(1-100)	______

UTPUT (Run)

1	SLP %	Slope steepness	pct	______
2	SLP DEG	Slope steepness	degrees	______
3	EL DIFF	Elevation change	feet	______
4	HORIZ DIST	Horizontal distance	feet	______

nput only for scale option = 1.
nput only for scale option = 2.

WIND ADJUSTMENT MODULE (English Units)

(Keywords: Input, List, Run, Quit)

INPUT (Input, List)

1	20'W	20-ft windspeed	[0-99 mi/h]	______	______	______
2	EXPOSURE	Exposure to wind 1 = exposed 2 = partially sheltered 3 = fully sheltered, open stand 4 = fully sheltered, closed stand 5 = enter wind adjustment factor	(1-5)		______	
3	WAF	[1]Wind adjustment factor	(0-1)		______	
4	MODEL #	[2]Fuel model number	(1-99)		______	

OUTPUT (Run)

1	MFWS	Midflame windspeed	mi/h	______	______	______

[1]Input only for exposure = 5.
[2]Input only for exposure = 1.

RH MODULE (English Units)

(Keywords: Input, List, Run, Quit)

INPUT (Input, List)

1	DRYB	Dry bulb temperature	[33-120 °F]	______	______	______
2	WETB	Wet bulb temperature	[0-120 °F]	______	______	______
3	EL	Elevation	[0-12,000 ft]	______	______	______

OUTPUT (Run)

1	%RH	Relative humidity	pct	______	______	______
2	DEWP	Dew point	°F	______	______	______

ERROR CODES:

-888 = Wet bulb temperature greater than dry bulb temperature

-999 = Dew point too cold for valid calculations

TABLE NO. 1 TABLE ITEM: %RH ROW ITEM ______ COL. ITEM ______

Column Values: ______ ______ ______

Row No.	Row Value	Table Values		
1	______	______	______	______
2	______	______	______	______
3	______	______	______	______

TABLE NO. 2 TABLE ITEM: DEWP ROW ITEM ______ COL. ITEM ______

Column Values: ______ ______ ______

Row No.	Row Value	Table Values		
1	______	______	______	______
2	______	______	______	______
3	______	______	______	______

TWO MODULE (English Units)

(Keywords: Input, List, Run, Quit)

PASSED FROM DIRECT (List)

1	MODEL1	First model run by DIRECT			______	
2	MODEL2	Second model run by DIRECT			______	
3	ROS1	Spread rate for first model		______	______	______
4	ROS2	Spread rate for second model		______	______	______

INPUT (Input, List)

5	COV1	Percent area coverage first model	[20-80%]	______	______	______

OUTPUT (Run)

1	ROS	Rate of spread	ch/h	______	______	______

TABLE NO. 1 TABLE ITEM: Weighted ROS ROW ITEM ______ COL. ITEM ______

Column Values: ______ ______ ______

Row No.	Row Value	Table Values		
1	______	______	______	______
2	______	______	______	______
3	______	______	______	______

OUTPUT TABLES

LIST NUMBER ______________

TABLE NO. ______ TABLE ITEM: ____________________ ROW ITEM __________ COL. ITEM ______

Column Values: __________ __________ __________

ow No.	Row Value	Table Values		
1	______	______	______	______
2	______	______	______	______
3	______	______	______	______

TABLE NO. ______ TABLE ITEM: ____________________ ROW ITEM __________ COL. ITEM ______

Column Values: __________ __________ __________

ow No.	Row Value	Table Values		
1	______	______	______	______
2	______	______	______	______
3	______	______	______	______

TABLE NO. ______ TABLE ITEM: ____________________ ROW ITEM __________ COL. ITEM ______

Column Values: __________ __________ __________

ow No.	Row Value	Table Values		
1	______	______	______	______
2	______	______	______	______
3	______	______	______	______

APPENDIX B: DATA SHEETS, METRIC UNITS OF MEASURE

FUEL MODEL MODULE (Metric)

(Keywords: Get, Input, List, Save, Quit, List Models, Delete Models)

INPUT LIST (Input, List)

1	MODEL #	Fuel model number	(14 - 99)	______
2	NAME	Fuel model name	(22 char. max.)	______
3	1HR LOAD	1-hour load	(0.02-70 M tons/ha)	______
4	10HR LOAD	10-hour load	(0-70 M tons/ha)	______
5	100HR LOAD	100-hour load	(0-70 M tons/ha)	______
6	HERB LOAD	Live herb load	(0-70 M tons/ha)	______
7	WOOD LOAD	Live woody load	(0-70 M tons/ha)	______
8	1HR S/V	1-hour surface/volume ratio	(40-120 cm^2/cm^3)	______
9	HERB S/V	[1]Herb surface/volume ratio	(40-120 cm^2/cm^3)	______
10	WOOD S/V	[2]Woody surface/volume ratio	(40-120 cm^2/cm^3)	______
11	DEPTH	Fuel bed depth	(1-300 cm)	______
12	HEAT	Fuel heat content	(15,000-30,000 joules/g)	______
13	MOIS EXT	Dead fuel extinction moisture	(10 - 50%)	______
14	STATIC-DYNAM	Static or dynamic model 0 = static or herb load is zero 1 = dynamic	(0 or 1)	______
15	WIND FACTOR	Exposed fuel wind adjustment factor	(0.01 - 1)	______

[1]Input only if herb load is greater than zero.
[2]Input only if wood load is greater than zero.

USER FUEL MODEL FILE CONTENTS (List Models)

Model Number	Model Name (22 characters maximum)

DIRECT MODULE (Metric)

LIST NUMBER ____________

(Keywords: Input, List, Run, Quit, SIze, SCorch, MAp, TWo)

INPUT (Input, List)

1	MODEL #	Fuel model number	(1-99)		______	
2	1H	1-H fuel moisture	[1-60%]	______	______	______
3	10H	[1]10-H fuel moisture	[1-60%]	______	______	______
4	100H	[1]100-H fuel moisture	[1-60%]	______	______	______
5	HERB	[1]Live herb moisture	[30-300%]	______	______	______
6	WOOD	[1]Live woody moisture	[30-300%]	______	______	______
7	MFWS	Midflame windspeed	[0-160 km/h]	______	______	______
8	SLP	Slope	[0-100% or 0-45 degrees]	______	______	______
9	WDIR	[2]Direction of wind vector, deg. clockwise from uphill	[0-360 degrees]	______	______	______
	PREDICT AT MAX		(Y/N)		______	
10	SDIR	Direction of spread calc., deg. clockwise from uphill (or from wind vector if slope is zero)	[0-360 degrees]	______	______	______

OUTPUT (Run)

0		No more tables				
1	ROS	Rate of spread	m/min	______	______	______
2	H/A	Heat per unit area	kjoules/m^2	______	______	______
3	FLI	Fireline intensity	kwatts/m	______	______	______
4	FL	Flame length	m	______	______	______
5	RI	Reaction intensity	kwatts/m^2	______	______	______
6	EWS	Effective windspeed in direction SDIR	km/h	______	______	______
7	MAXD	[3]Direction of maximum spread, deg. clockwise from uphill	degrees	______	______	______

[1]Input only if corresponding fuel load is not zero.
[2]Input only if midflame windspeed (MFWS) and slope (SLP) are not zero.
[3]Output only if calculations are in direction of maximum spread.

SIZE MODULE (Metric)

LIST NUMBER ______________

(Keywords: Input, List, Run, MAp, [1]COntain, Quit)

PUT (Input, List)

1	ROS	[2]Rate of spread	[0.03-170 m/min]	____	____	____
2	EWS	[2]Effective windspeed	[0-160 km/h]	____	____	____
3	ET	Elapsed time	[0.1 - 8 h]	____	____	____

JTPUT (Run)

0		No more tables				
1	AREA	Area	ha	____	____	____
2	PER	Perimeter	m	____	____	____
3	L/W	Length-to-width ratio		____	____	____
4	FSD	Forward spread distance	m	____	____	____
5	BSD	Backing spread distance	m	____	____	____
6	MXW	Maximum fire width	m	____	____	____

ZE can link to CONTAIN only if linked to DIRECT.
put only when SIZE is used as an independent module.

CONTAIN MODULE (Metric)

LIST NUMBER ____________

(Keywords: Input, List, Run, Quit)

INPUT	(Input, List)					
1	RUN OPT	Run option 1 = calculate total line building rate 2 = calculate burned area	(1 or 2)		______	
2	ATTACK OPT	Attack option 1 = head 2 = rear	(1 or 2)		______	
3	ROS	[1]Rate of spread	[0.03-170 m/min]	______	______	______
4	AREA	[1]Initial fire area	[0.05-50 ha]	______	______	______
5	L/W	[1]Length-to-width ratio	[1-5]	______	______	______
6	BAT	[2]Burned area target	[0.1-1000 ha]	______	______	______
7	TLBR	[3]Total line building rate	[0.1-250 m/min]	______	______	______
OUTPUT	(Run)					
1	PER	Total length of line	m	______	______	______
2	TIME	Containment time	hours	______	______	______
3	FFS	[4]Final fire size	ha	______	______	______
3	TLBR	[5]Total line building rate	m/min	______	______	______
4	MAXA	[5]Maximum area calculable	ha	______	______	______
5	MINA	[5]Minimum area calculable	ha	______	______	______

Error Codes:

- −1 = Burned area target too large, cannot calculate slow enough line building rate
- −2 = Line building rate too slow to catch fire
- −3 = L/W ratio too large
- −4 = Burned area target too close to initial fire size
- −5 = Line building rate too fast

[1]Input only when CONTAIN is used as an independent module.
[2]Input only for run option = 1 (calculate total line building rate).
[3]Input only for run option = 2 (calculate burned area target).
[4]Output only for run option = 2.
[5]Output only for run option = 1.

SPOT MODULE (Metric)

LIST NUMBER ____________

(Keywords: Input, List, Run, MAp, Quit)

UT (Input, List)

1	BRAND SRC	Firebrand source 1 = torching trees 2 = burning piles 3 = wind-driven surface fire	(1-3)		____	
2	MCHT	Mean cover height	[0-100 m]	____	____	____
3	10MW	10-meter windspeed	[0-160 km/h]	____	____	____
4	RVEL	Ridge-to-valley elevation difference	[0-1,500 m]	____	____	____
5	RVHD	Ridge-to-valley horiz. distance	[0-6 km]	____	____	____
6	SRC LOC	Spotting source location 0 = midslope, windward side 1 = valley bottom 2 = midslope, leeward side 3 = ridgetop	(0-3)		____	
7	TREE SP	[1]Tree species 1 = Engelmann spruce 2 = Douglas-fir, subalpine fir 3 = hemlock 4 = ponderosa, lodgepole pine 5 = white pine 6 = balsam fir, grand fir	(1-6)		____	
8	DBH	[1]Torching tree DBH	[10-100 cm]	____	____	____
9	TRHT	[1]Torching tree height	[1-100 m]	____	____	____
10	#TR	[1]Number of torching trees	[1-30]	____	____	____
11	FLHT	[2]Continuous flame height	[0.1-30 m]	____	____	____
12	FL	[3]Flame length	[0.03-15 m]	____	____	____
13	MODEL #	[3]Fuel model	(1-99)		____	
14	HERB	[4]Herbaceous moisture	[30-300%]	____	____	____

ITPUT (Run)

1	SPOT	Maximum spotting distance	km	____	____	____

ɔut only for firebrand source = 1 (torching tree option).
ɔut only for firebrand source = 2 (burning pile option).
[3]Input only for firebrand source = 3 (wind-driven surface fire option).
[4]Input only for dynamic fuel models with a herbaceous fuel load.

SCORCH MODULE (Metric)

(Keywords: Input, List, Run, Quit)

INPUT (Input, List)

1	TEMP	Ambient air temperature	[0-50 °C]			
2	FL	[1]Flame length	[0.03-5 m]			
3	MFWS	[1]Midflame windspeed	[0-16 km/h]			

OUTPUT (Run)

1	SCHT	Scorch height	m			

[1]Input only if SCORCH is used as an independent module.

TABLE NO. 1 TABLE ITEM: Scorch height ROW ITEM ______ COL. ITEM ______

Column Values: ______ ______ ______

Row No.	Row Value	Table Values		
1				
2				
3				

IGNITE MODULE (Metric)

(Keywords: Input, List, Run, Quit)

IPUT (Input, List)

1	TEMP	Ambient air temperature	[0-50 °C]	______	______	______
2	1H	1-h fuel moisture	[1-60%]	______	______	______
3	SHAD	Shade	[0-100%]	______	______	______

UTPUT (Run)

1	P(I)	Probability of ignition	pct	______	______	______

TABLE NO. 1 TABLE ITEM: Prob. of Ignition ROW ITEM ______ COL. ITEM ______

Column Values: ______ ______ ______

ow No.	Row Value	Table Values		
1	______	______	______	______
2	______	______	______	______
3	______	______	______	______

MOISTURE MODULE (Metric)

LIST NUMBER ____________

(Keywords: Input, List, Run, Quit)

INPUT	(Input, List)			
1	RUN OPT	Run option 1 = Burn time calculations 2 = Hourly calculations	(1 or 2)	____
TIME AND LOCATION				
2	BURN MONTH	Month of burn	(1-12)	____
3	BURN DAY	Day of burn	(1-31)	____
4	LATITUDE	Latitude of fire location	(−90 to 90 degrees)	____
5	BURN TIME	Time of burn	(0-2,359 h)	____
FUEL MODEL				
6	MODEL #	Fuel model number	(1-99)	____
SLOPE, ELEVATION, ASPECT				
11	SLP	Slope steepness	[0-100% or 0-45 degrees]	____ ____ ____
12	ELFL	Elevation of fire location	[0-4,000 m]	____ ____ ____
	RH OBS AT FIRE		(Y/N)	____
13	ELOB	Elevation of T&RH observations	(0-4,000 m)	____
14	ASPECT	Aspect of fire location 0 = north 180 = south 90 = east 270 = west	(0-360 degrees)	____
TIMBER OVERSTORY DESCRIPTION				
15	CCLO	Crown closure	[0-100%]	____ ____ ____
16	FOLIAGE	Foliage presence 0 = absent 1 = present	(0 or 1)	____
17	SHADE TOL	Shade tolerance 0 = intolerant 1 = tolerant	(0 or 1)	____
18	DOM TYPE	Dominant tree type 1 = coniferous 2 = deciduous	(1 or 2)	____
19	AVHT	Average tree height	[3-100 m]	____ ____ ____
20	H/H	Crown height/tree height ratio	[0.1-1]	____ ____ ____
21	H/D	Crown height/crown diameter ratio	[0.2-5]	____ ____ ____

MOISTURE MODULE (continued, Metric)

LIST NUMBER ____________

RLY AFTERNOON WEATHER

22	14T	Burn day 1400 temperature	[0-50 °C]	______	______	______
23	14RH	Burn day 1400 relative humidity	[1-100%]	______	______	______
24	14W	Burn day 1400 10-meter windspeed	[0-160 km/h]	______	______	______
25	14CC	Burn day cloud cover	[0-100%]	______	______	______
26	14HZ	Burn day 1400 haziness	[1-4]	______	______	______

1 = very clear sky
2 = average clear forest atmosphere
3 = moderate blue haze
4 = dense haze—moderate smoke

NSET WEATHER

27	SST	Sunset temperature	[0-50 °C]	______	______	______
28	SSRH	Sunset relative humidity	[1-100%]	______	______	______
29	SSW	Sunset 10-meter windspeed	[0-160 km/h]	______	______	______
30	SSCC	Sunset cloud cover	[0-100%]	______	______	______

NRISE WEATHER

31	SRT	Sunrise temperature	[0-50 °C]	______	______	______
32	SRRH	Sunrise relative humidity	[1-100%]	______	______	______
33	SRW	Sunrise 10-meter windspeed	[0-160 km/h]	______	______	______
34	SRCC	Sunrise cloud cover	[0-100%]	______	______	______

RN TIME WEATHER

35	BTT	Burn time temperature	[0-50 °C]	______	______	______
36	BTRH	Burn time relative humidity	[1-100%]	______	______	______
37	BTW	Burn time 10-meter windspeed	[0-160 km/h]	______	______	______
38	BTCC	Burn time cloud cover	[0-100%]	______	______	______
39	BTHZ	Burn time haziness	[1-4]	______	______	______

1 = very clear sky
2 = average clear forest atmosphere
3 = moderate blue haze
4 = dense haze—moderate smoke

MOISTURE MODULE (continued, Metric)

LIST NUMBER ________

BURN TIME WIND

40	EXPOSURE	Exposure of fuels to wind 1 = exposed 2 = partially sheltered 3 = fully sheltered—open stand 4 = fully sheltered—dense stand 5 = direct entry of wind adjustment factor	(1-5)	____
41	WAF	Wind adjustment factor Exposure 5 only	(0-1)	____

MOISTURE INITIALIZATION OPTION

43	MOIS OPT	Moisture initialization option 1 = fine fuel moisture known for day before burn 2 = not allowed 3 = incomplete data; rain the week before burn 4 = incomplete data; no rain the week before burn 5 = incomplete data; weather pattern changing	(1-5)	____

MOISTURE OPTION 1

44	FM-1	Burn day-1 fine fuel moisture	[1-100%]	____ ____ ____

MOISTURE OPTION 3

51	RDAY	Number of days before burn that rain occurred	[1-7 days]	____ ____ ____
52	RAIN	Rain amount, millimeters	[0-100 mm]	____ ____ ____
53	RDT	1400 temperature on rain day	[0-50 °C]	____ ____ ____
54	SKY CODE	Sky condition from rain day to burn day 1 = clear 2 = cloudy 3 = partly cloudy	(1-3)	____

MOISTURE OPTION 4

No additional input.

MOISTURE MODULE (continued, Metric)

LIST NUMBER ______

MOISTURE OPTION 5

55	TD-1	Burn day −1 1400 temperature	[0-50 °C]	____	____	____
56	RD-1	Burn day −1 1400 relative humidity	[1-100%]	____	____	____
57	WD-1	Burn day −1 1400 10-meter windspeed	[0-160 km/h]	____	____	____
58	CD-1	Burn day −1 1400 cloud cover	[0-100%]	____	____	____
59	WTHR	Weather condition prior to burn day −1 1 = hot and dry 2 = cool and wet 3 = between 1 and 2	[1-3]	____	____	____

OUTPUT (Run)

1	MOIS	1-hour fuel moisture	pct	____	____	____
2	TEMP	Fuel level temperature	°C	____	____	____
3	%RH	Fuel level relative humidity	pct	____	____	____
4	SHAD	Percent of area shaded	pct	____	____	____
5	P(I)	Probability of ignition	pct	____	____	____

MOISTURE MODULE (continued, Metric)

LIST NUMBER ______

HOURLY OUTPUT (Run)

TIME	FMOIST pct	FTEMP °C	FRH pct
14			
15			
16			
17			
18			
19			
20			
21			
22			
23			
24			
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			
11			
Burn Time ______			

MAP MODULE (Metric)

LIST NUMBER ____________

(Keywords: Input, List, Run, Quit)

'UT LIST (Input, List)

1	SCL OPT	[1]Scale option 1 = Representative fraction			1	
2	RF/1000	Representative fraction/1,000 e.g., RF of 1/100,000 = 100	(1-500)			
4	UNITS OPT	Units option 1 = Spread distance 2 = Spot distance 3 = Rate of spread	(1-3)			
5	DIST	[2]Spread distance	[0-20,000 m]			
6	SPOT	[3]Spot distance	[0.1-15 km]			
7	ROS	[4]Rate of spread	[0.03-170 m/min]			
8	TIME	[4]Elapsed time	[0.1-8 h]			
5	FSD	[5]Forward spread distance	m			
6	BSD	[5]Backing spread distance	m			
7	MXW	[5]Maximum fire width	m			

TPUT (Run)

1	MFSD	Forward spread distance on map (UNITS OPT = 1 or 3)	cm			
1	MSPT	Forward spot distance on map (UNITS OPT = 2)	cm			
2	MBSD	Backing spread distance on map (SIZE linked only)	cm			
3	MMXW	Maximum fire width on map (SIZE linked only)	cm			

tric option sets the scale option = 1 (representative fraction).
ut only for units option = 1.
ut only for units option = 2.
ut only for units option = 3.
ssed from SIZE for linked run only. No input is needed.

SLOPE MODULE (Metric)

LIST NUMBER ______________

(Keywords: Input, List, Run, Quit)

From Point _____ to Point _____

INPUT LIST (Input, List)

1	SCL OPT	[1]Scale option 1 = Representative fraction		1
2	RF/1000	[1]Representative fraction/1,000 e.g., RF of 1/100,000 = 100	(1-500)	______
4	CON INT	Contour interval	(1-200 m)	______
5	MAP DIST	Map distance	(0.1-25 cm)	______
6	# INTVLS	Number of contour intervals	(1-100)	______

OUTPUT (Run)

1	SLP %	Slope steepness	pct	______
2	SLP DEG	Slope steepness	degrees	______
3	EL DIFF	Elevation change	m	______
4	HORIZ DIST	Horizontal distance	m	______

[1]Metric option sets the scale option = 1 (representative fraction).

WIND ADJUSTMENT MODULE (Metric)

(Keywords: Input, List, Quit)

PUT LIST (Input, List)

1	10MW	10-meter windspeed	[0-160 km/h]	______	______	______
2	EXPOSURE	Exposure to wind 1 = exposed 2 = partially sheltered 3 = fully sheltered, open stand 4 = fully sheltered, closed stand 5 = enter wind adjustment factor	(1-5)		______	
3	WAF	[1]Wind adjustment factor	(0-1)		______	
4	MODEL #	[2]Fuel model number	(1-99)		______	

TPUT (Run)

1	MFWS	Midflame windspeed	km/h	______	______	______

ut only for exposure = 5.
ut only for exposure = 1.

RH MODULE (Metric)

(Keywords: Input, List, Run, Quit)

INPUT LIST (Input, List)

1	DRYB	Dry bulb temperature	[0-50 °C]	____	____	____
2	WETB	Wet bulb temperature	[−18 to 50 °C]	____	____	____
3	EL	Elevation	[0-4,000 m]	____	____	____

OUTPUT (Run)

1	%RH	Relative humidity	pct	____	____	____
2	DEWP	Dew point	°C	____	____	____

ERROR CODES:

−888 = Wet bulb temperature greater than dry bulb temperature

−999 = Dew point too cold for valid calculations

TABLE NO. 1 TABLE ITEM: %RH ROW ITEM ____ COL. ITEM ____

Column Values: ____ ____ ____

Row No.	Row Value	Table Values		
1	____	____	____	____
2	____	____	____	____
3	____	____	____	____

TABLE NO. 2 TABLE ITEM: DEWP ROW ITEM ____ COL. ITEM ____

Column Values: ____ ____ ____

Row No.	Row Value	Table Values		
1	____	____	____	____
2	____	____	____	____
3	____	____	____	____

TWO MODULE (Metric)

(Keywords: Input, List, Run, Quit)

ASSED FROM DIRECT (List)

1	MODEL1	First model run by DIRECT			______	
2	MODEL2	Second model run by DIRECT			______	
3	ROS1	Spread rate for first model		______	______	______
4	ROS2	Spread rate for second model		______	______	______

PUT (Input, List)

5	COV1	Percent area coverage first model	[20-80%]	______	______	______

JTPUT (Run)

1	ROS	Rate of spread	m/min	______	______	______

TABLE NO. 1 TABLE ITEM: Weighted ROS ROW ITEM ______ COL. ITEM ______

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OUTPUT TABLES

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Susott, Ronald A.; Burgan, Robert E. Fire behavior computations with the Hewlett-Packard HP-71B calculator. General Technical Report INT-202. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986. 80 p.

This report describes the operation of the fire behavior prediction program available as a Custom Read Only Memory (CROM) for the Hewlett-Packard model 71B handheld calculater. Worked examples are given for each of the 13 program modules, and the inputs and outputs are described. "Fire danger computations with the Hewlett-Packard HP-71B calculator," by Robert E. Burgan and Ronald A. Susott (1986) is a separate publication describing National Fire-Danger Rating (NFDR) system computations with the HP-71B.

KEYWORDS: fire behavior prediction, calculation aids, metric

INTERMOUNTAIN RESEARCH STATION

The Intermountain Research Station provides scientific knowledge and technology to improve management, protection, and use of the forests and rangelands of the Intermountain West. Research is designed to meet the needs of National Forest managers, Federal and State agencies, industry, academic institutions, public and private organizations, and individuals. Results of research are made available through publications, symposia, workshops, training sessions, and personal contacts.

The Intermountain Research Station territory includes Montana, Idaho, Utah, Nevada, and western Wyoming. Eighty-five percent of the lands in the Station area, about 231 million acres, are classified as forest or rangeland. They include grasslands, deserts, shrublands, alpine areas, and forests. They provide fiber for forest industries, minerals and fossil fuels for energy and industrial development, water for domestic and industrial consumption, forage for livestock and wildlife, and recreation opportunities for millions of visitors.

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A ril 1986

Proceedings— Conifer Tree Seed in the Inland Mountain West Symposium

Missoula, Montana, August 5-6, 1985

FOREWORD

The symposium "Conifer Tree Seed in the Inland Mountain West" started, developed, and matured in much the same manner and time frame as many conifer cone crops. Like the biological stresses that often stimulate cone production, the stress of knowledge needs prompted the initiation of this symposium.

The first suggestion that a symposium be held to consolidate the available cone and seed knowledge came at a January 27, 1983, meeting of Forest Service Intermountain Station and Northern Region scientists discussing cone and seed production information needed to enhance natural and artificial regeneration in the Northern Rockies. Like the initiation of a cone bud, the idea for a symposium was nothing really new, it just came at the right time and fell into a fertile environment of silviculturists, geneticists, and entomologists.

A steering committee, chaired by Dr. Raymond C. Shearer of the Intermountain Research Station, was formed and proceeded with the planning. Committee members were: Dr. George Blake, School of Forestry, University of Montana; Mr. Jerald E. Dewey, Pest Management, Northern Region, Forest Service; Dr. A. K. Hellum, Department of Forest Science, University of Alberta; Dr. George E. Howe, Division of Timber Management, Northern Region, Forest Service; and Mr. Wayne Maahs, Forestry Division, Champion International Corporation. The School of Forestry and Center for Continuing Education of the University of Montana handled many of the logistical details for the symposium and the Intermountain Research Station edited and published the proceedings.

Numerous meetings, letters, announcements, coordination sessions with authors, and a host of other details preceded the very successful symposium, August 5-6, 1985. Included were 40 papers presented by silviculturists, geneticists, entomologists, physiologists, pathologists, nurserymen, and others. The objective of the symposium--to consolidate information and research conducted on conifer tree cones and seeds native to the Inland Mountain West of the United States and Canada--was met, and 164 attendees left with a much better idea of what is known about western conifers. This symposium culminated efforts of many people, and, like a cone that survives all the hazards and produces seed at the end of its development period, succeeded in producing a very viable proceedings.

Wyman C. Schmidt, Silviculture Project Leader
Intermountain Research Station
Forest Service, U.S. Department of Agriculture
Bozeman, MT

Proceedings—Conifer Tree Seed in the Inland Mountain West Symposium

Missoula, Montana, August 5-6, 1985

Compiler:

RAYMOND C. SHEARER, Research Forester, Intermountain Research Station, Missoula, Montana

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CONTENTS

SEED CONSERVATION PROBLEMS: NATURAL AND UNNATURAL

J. Derek Bewley and Andrew D. Powell

ABSTRACT: The majority of seeds respond to storage conditions in an "orthodox" manner, in that a low seed moisture content and low temperature prolong their storage life. Deterioration can take place in the seemingly "dry" stored seeds, perhaps largely due to physico-chemical processes. The consequences of deterioration to metabolic integrity of the seeds are various, but macromolecular damage, leading to defective membranes and damaged organelles are manifestations. Storage of seeds in the imbibed state, a condition in which many seeds find themselves in "natural" storage conditions in seed-soil banks, may prolong their longevity. Hydration may allow the seeds to put into operation the repair mechanisms essential for the maintenance of their metabolic integrity. The cost, however, is the consumption of reserves to provide energy, which may eventually become depleted. Recalcitrant seeds cannot withstand drying and must be stored in a wet state. These latter seeds might persist better as seedlings, and the preservation of difficult seed species (both orthodox and recalcitrant) in seedling banks is a possible strategy.

INTRODUCTION

The seed is the dispersal stage of the plant life cycle and, in many instances, it is the only stage which can survive severely adverse environmental conditions. A low water content (usually some 5-15%), combined with an inherent ability of the cells to withstand severe water loss, facilitate the seed's survival. In the dry state, many seeds can withstand extremes of cold (storage in liquid nitrogen is becoming an increasingly common practice for genetic stocks of seeds) and heat (on the desert floors temperatures may exceed 75°C). As a general rule, commercial storage of seeds takes advantage of their ability to retain metabolic quiescence in the dry state, although other factors must be considered, as will be discussed later.

Paper presented at the Conifer Tree Seed in the Inland Mountain West Symposium, Missoula, MT, August 5-6, 1985.

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Seeds which retain their viability in the dry state, and can be stored thus, are regarded as conforming to the general "rules" for storage conditions; such seeds are described as showing orthodox viability characteristics. The seeds of all common agricultural and horticultural crop species which are annual or biennial exhibit this orthodox storage behaviour. There is another group of species, however, which produce seeds that normally never dry out on the mother plant, which are dispersed in the moist condition, and which are killed if their moisture content declines below some relatively high critical value. Since these seeds do not conform to the rules of storage that are applicable to the orthodox ones, such desiccation-tolerant seeds have been designed as recalcitrant (Roberts 1973).

In this paper we will consider some of the problems associated with the storage of orthodox seeds in the dry state--a common practice, but an unnatural condition for many seeds to find themselves in for protracted periods. More naturally, when many seeds are shed from the mother plant they remain buried in the substrate, often in an intermittently wet state. Such seeds can withstand drying, however, which is in contrast to the situation in recalcitrant seeds, for these must be kept constantly in a near-hydrated state.

ORTHODOX SEEDS AND DRY STORAGE

Premature Drying of Seeds for Storage

Acquisition of desiccation-tolerance during seed development occurs approximately at the midway stage, e.g. in Ricinus communis (Kermode and Bewley 1985a), Pisum sativum (Rogerson and Matthews 1977), and Glycine max (Adams and others 1983). Prior to this time, premature desiccation generally results in poor recovery of germinability of the seed upon subsequent rehydration. There is a concomitant reduction in the metabolic capacity of the seed, e.g. for protein synthesis, when one attempts to germinate seeds following drying during this desiccation-intolerant stage (Dasgupta and others 1982). Immature seeds exhibit a great variation in the rate of water loss that they can tolerate. Thus, when we refer to a developing seed acquiring desiccation-tolerance, we must define also the rate of water loss tolerated. For example, Phaseolus vulgaris seeds can tolerate extreme rates of drying, i.e. rapid desiccation over activated silica gel (Dasgupta and others 1982), from about the 26th day of development (of a 42-day developmental cycle), whereas in R. communis tolerance of such extreme rates

of water loss is not acquired until the 55th day of a 60-day developmental cycle (Kermode and Bewley 1985a). On the other hand, this latter seed can withstand slow water loss, even to complete desiccation, at a stage less than half-way through its development, and can germinate fully upon subsequent rehydration. Seeds of Glycine max also require slow dehydration (which can be achieved while they are in the pod) to survive premature drying; those shelled before drying lose their viability (Fjerstad and others 1981; Adams and others 1983). The advantage of the slow water loss is that it may permit membranous structures within cells to undergo certain reversible conformational changes during desiccation, thus allowing them to retain their integrity (Bewley 1979; Fjerstad and others 1981). Thus, upon rehydration, metabolism within reasonably intact cells can recommence, and the appropriate germination mechanisms can be put rapidly into effect. Rapid drying of immature seeds, on the other hand, may lead to irreversible cellular changes which are too extensive for repair to be effected in the germinating seed, with a consequent decline in, or loss of, viability.

Premature harvesting of seeds while in the desiccation-tolerant stage of development might be advantageous, in some instances, for the subsequent establishment and growth of the progeny. Studies on the endosperms of developing seeds of R. communis (Kermode and Bewley 1985b) show, for example, that synthesis of certain protein fractions (including the soluble and major insoluble storage proteins) reaches a peak at about the midway point of development (fig. 1A). Later in development protein synthetic activity declines; after 45-50 days of development this decline is because the seed is drying out as it reaches the latter stages of maturation. Hence the seed's synthetic potential changes with time during development. When the seed is dried prematurely at 30 days of development it survives, and upon rehydration its rate of synthetic activity is considerably higher than in germinating mature dry seeds or in 40-day dried and rehydrated seeds (fig. 1B). Hence there is a strong correlation between the competence of the seed to conduct protein synthesis prior to premature drying and its competence to carry out this synthesis upon subsequent rehydration--even though the products of protein synthesis formed during development and germination are very different (Kermode and Bewley 1985b; Kermode and others 1985). If the high synthetic capacity also has a bearing on the survivability and germinability of seeds (i.e. if there is increased viability because of an increased potential for synthetic activity) then it might be of value to harvest certain species of seeds prematurely, during the desiccation-tolerant stage, when the capacity for cellular activity of the seeds is highest. Following the appropriate drying regimes, and under suitable storage conditions, the chances of maintaining seed viability might be greater.

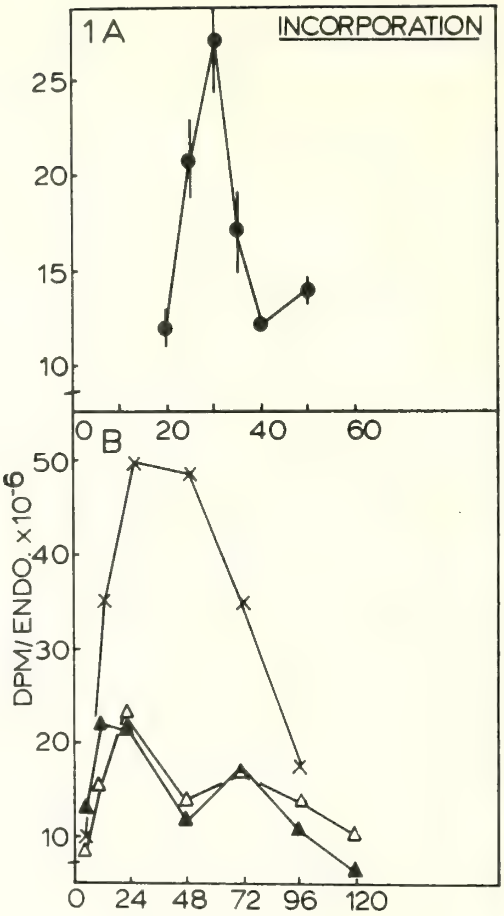

Figure 1.--Incorporation of ^{3}H-leucine into (A) developing seeds of Ricinus communis harvested a 20-50 days after pollination (DAP) and (B) following mature seed imbibition 5-120 hours after imbibition (HAI) (▲); following rehydratio of desiccated 40 DAP seeds, 5-120 HAI (△); and following rehydration of desiccated 30 DAP seeds 5-120 HAI (X). Note that the high synthetic activity of 30 DAP seeds is maintained upon rehydration following premature desiccation. After Kermode and Bewley (1985b).

Some studies have been carried out to determine if the maturity and quality of tree seeds at the time of collection have an effect upon subsequent germinability. The general consensus appears to be that early harvesting is not necessarily advantageous and, indeed, in some instances it may be disadvantageous (Wang and others 1982). In no case, however, were correlations made with metabolic activity during development, nor was storeability of the seeds a factor under consideration.

Viability of Seeds in Dry Storage: Optimizing Conditions

The majority of seed species are of the orthodox kind in relation to storage and conform to certain general rules that predict the pattern c loss of viability in relation to their storage environment (Harrington 1973).

Rule 1 states that for each 1% decrease in seed moisture content the storage life of the seed is doubled;

Rule 2 states that for each 10°F (5.6°C) decrease in seed storage temperature the storage life of the seed is doubled;

And Rule 3 combines these observations to state that the sum of the storage temperature in degrees F and percent relative humidity (RH) must not exceed 100, with no more than 50% of the sum being contributed by the temperature.

At high seed moisture contents (>30%) non-dormant seeds will germinate, and from 18-30% moisture content rapid deterioration by microorganisms may occur, particularly in the presence of oxygen. Fungi will grow on seeds at 10-18% moisture content, and above 18% the stored seeds may respire and deplete essential reserves. An additional problem arises under conditions of poor aeration, for both seed and fungal respiration could generate enough heat to kill the seeds. Below about 10% moisture content insect activity is diminished, and at 5-7% moisture content the seeds are metabolically quiescent. A low moisture content of 4-5% seems to be less desirable for long-term storage than one of 6-7%, for reasons which are not abundantly clear.

The use of cold temperatures in storage has a generally beneficial effect on longevity. At liquid nitrogen temperatures seeds may survive indefinitely (Stanwood and Bass 1981). Longevity at -20°C for many seeds is considerably prolonged --the required regeneration interval for Pisum sativum stored at -20°C and 5% moisture content may exceed 1000 years, for example (Roberts and Ellis 1977). Even storage at 0-5°C will improve the longevity of seeds, as would be predicted by Rule 2, provided that certain precautions are taken--particularly ensuring that the stored seeds do not pick up moisture resulting from increased atmospheric humidity at low temperatures.

The extension of the interval between successive regenerations of seed stocks in storage has been a major aim. This not only eliminates the need to devote time (and money) into seed stock regeneration but also eliminates the rate of genetic drift which might take place in the small seed batches planted out from the stored stocks. Repeated regenerations can also put the seed stock at risk of diseases and other environmental stresses which might prove to be fatal.

While considerable attention has been paid to results from germination tests, more recently there has come the appreciation that seed batches with the same germinability can perform differently in the field, i.e. seed batches with similar viabilities have different vigour levels. The International Seed Testing Association has defined seed vigour as "the sum total of those properties of the seed which determine the potential level of activity and performance of the seed or seed lot during germination and seedling emergence" (Perry 1978). Vigour tests have been developed (Perry 1981) which when used in conjunction with the standard germination test allow the identification of a seed batch which might not establish a good stand after germination even though germination test values were the same. These tests identify the fact that deterioration in the performance of a seed can take place in storage even though high germination levels are maintained. As we shall see later, some metabolic lesions may contribute to a loss in vigour as well as viability, but handling of the seeds prior to harvest is also important. The long-term storage of a seed lot with an initial low vigour is a waste of precious resources.

The drying of mature seeds for storage can be problemmatical, particularly in cases where complete loss of water has not occurred on the mother plant. In the previous section we outlined how drying of prematurely harvested seeds may have to be carefully controlled. Such is also the case for some seeds harvested at 15-20% moisture content and then dried to some 5-7% moisture content for storage. Elevated temperatures during drying or drying too quickly or excessively can reduce viability and vigour, although under good management this should not occur (Rampton and Lee 1969). Care must also be taken during mechanical harvesting and processing to reduce the damage to the outer seed structures since this might lead to damage when imbibition takes place. The moisture content of seeds will play an important role in their ability to withstand harsh mechanical handling (Powell, A.A. and others 1984).

The viabilities expressed by populations of mature dry seeds before and during storage are very variable; for many agricultural and horticultural species it is usually, and acceptably, very high --in the range of 95-98%. Viabilities of other species, including forest species, are frequently much lower. In some instances relationships are to be found between mature seed characteristics and viability. In several Pinus spp., for example, there may be a correlation between mature seed weight and germination percentage, and also correlations with seedling vigour (Ghosh and others 1976; Kandya 1978), although this may not always be the case (Chauhan and Raina 1980). From a practical point of view, sorting of seeds by weight before planting may not be desirable, and it may be best to use all viable seeds for reforestation (Hellum 1976). The weight of white spruce seeds seems to be highly specific for an individual tree and thus there might be a reduction in genetic variability if seeds are sorted by weight.

Metabolic Changes Occurring During Seed Storage

We may wonder how a dry seed, in a state of metabolic torpor, can undergo deterioration in storage--and how this can be prevented. Under conditions where the cells of the seed are partially hydrated in storage a limited amount of metabolism might take place, which could be detrimental. Partial completion of anabolic or

catabolic pathways could lead to the accumulation of undesirable metabolites, resulting in a potentially fatal disequilibrium, which cannot be rectified upon subsequent reimbibition.

The metabolic manifestations of deterioration in dry storage are many, and have been detailed in several reviews (Bewley and Black 1982; Osborne 1980; Roberts 1975, 1981). A summary of the various metabolic lesions that occur during storage and which result in a loss of viability is presented in fig. 2. Any single lesion could result in a complete loss of germinability or simply a reduction in vigour, depending upon its quantitative expression within the cell. It is more likely, however, that aging elicits a number of distinct lesions (perhaps none of them fatal by themselves) which together reduce the seed's ability to survive.

Of the cellular changes which take place in the dry state, those to membranes have attracted the most interest. This is because the integrity of the plasmalemma and associated membranes (endoplasmic reticulum) is an integral requirement for normal cellular function, and efficient mitochondria are required for the maintenance of a favourable energy status. A loss of integrity of the plasmalemma and tonoplast in aged seeds is implied from observations that more substances leak into the imbibition medium from such seeds than from unaged ones (Ching and Schoolcraft 1968; Parrish and Leopold 1978). Excess leakage from deteriorated seeds may represent a loss of respirable substrate, but quantitative correlations between this loss and subsequent germinability have not been made. In some instances, increased leakage of organic metabolites might lead to a secondary damaging effect by stimulating growth of contaminating microorganisms on the seed surface.

The cause of the changes in membrane integrity during seed aging in storage has not been elucidated, and there is little agreement between workers on the deteriorative changes suffered by phospholipids, the major membrane component. In some seeds there is reasonable evidence that a decline in unsaturated fatty acids, e.g. linoleic and/or linolenic acids, can be correlated with loss of germinability, e.g. in slowly aged Glycine max (Priestley and Leopold 1983) and Trifolium subterraneum (Flood and Sinclair 1981). Seeds of Acer platanoides when subjected to an accelerated aging treatment (i.e. by being placed in a saturated atmosphere at 30°C) exhibit a marked decline in germination, which is accompanied by a loss of phosphatidyl choline and phosphatidyl glycerol from the membrane fraction (Pukacka 1983). The cause of the changes in fatty acid characteristics of dry seeds, and hence their loss of viability, has been attributed to physico-chemical perturbations of these molecular components of the membranes. In particular, peroxidation has been singled out as a major causative agent, with the auto-catalytic oxidation of unsaturated fatty acids (e.g. linoleic acid and linolenic acid) by atmospheric oxygen in a free-radical chain reaction occurring in the dry seed. However, the evidence for lipid peroxidation in aging seeds is tenuous, and that which is in its favour is largely circumstantial (Harman and Mattick 1976; Koostra and Harrington 1969).

There are enzyme (e.g. superoxide dismutase) and scavenger systems present within seeds which can reduce the activity of free radicals. Correlations between endogenous superoxide dismutase activity and viability of seeds have been attempted, but no definitive role can be assigned to this enzyme as far as the restriction of peroxidation is concerned (e.g. Stewart and Bewley 1980). Tocopherols are organic free radical scavengers and it is estimated that one molecule of this compound can afford antioxidant protection to several thousand fatty acid molecules. Attempts to correlate tocopherol levels with susceptibility to peroxidation damage have been without success; in aged soybean seeds, for example, tocopherol levels are the same as in

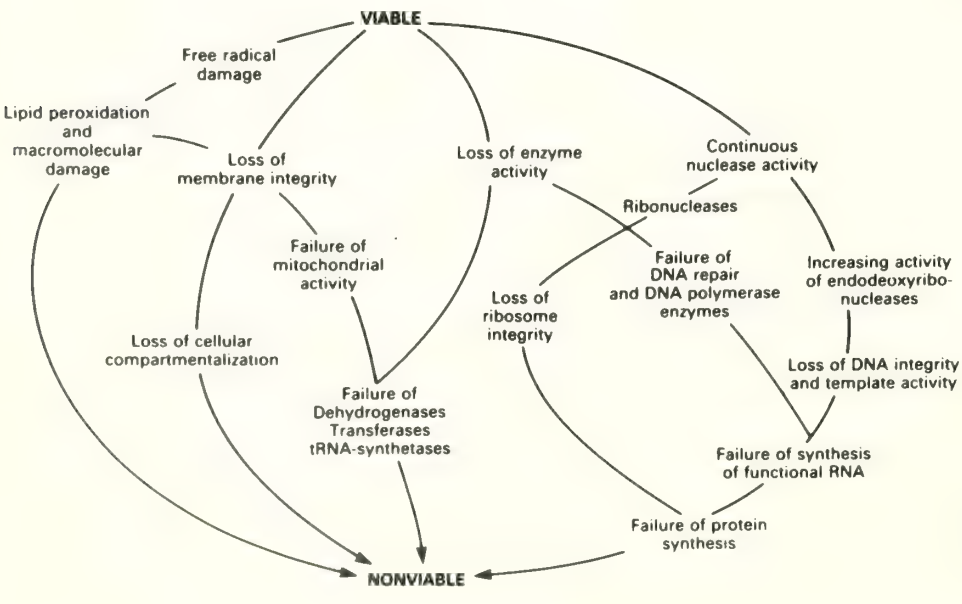

Figure 2.--A scheme to explain the potential causes for loss of viability in stored seeds. Adapted from Osborne (1980).

unaged controls (Priestley and others 1980; Fielding and Goldsworthy 1980). On the other hand, it appears to be beneficial to add anti-oxidants to isolated membrane preparations, or to seeds (Fielding and Goldsworthy 1980; Basu and Dasgupta 1978).

Some restorative treatments have been attempted to increase germinability of seeds subjected to loss of viability in dry storage. Hydration of seeds in atmospheres of high relative humidity before being placed in water is beneficial to unaged seeds (Simon and Raja Harun 1972; Powell and Matthews 1978), and may be of value in encouraging germination of aged ones. Improved germinability or growth of seeds with reduced viability or vigor can be achieved, for example, by subjecting them to conditions that permit low, or slow, water uptake, e.g. by "flash imbibition" of wheat (Goldsworthy and others 1982); by placing seeds in an atmosphere of high relative humidity (Basu and Pal 1980; Sanchez and Miguel 1983); or by imbibing seeds initially in an osmoticum, such as polyethylene glycol (Brocklehurst and Dearman 1983; Burgass and Powell 1984). Presumably the initial slow hydration of the seeds allows for the ordered rearrangement or repair of membranes before the inrush of water associated with imbibition from the dry state, which might otherwise be too sudden and disruptive.

Whatever the real causes of deterioration in dry storage are, it is evident that they take place while the seed is in a state of quiescence or near-quiescence, and while it has little chance to accommodate the changes which are taking place within its cells. Only inherent defense mechanisms, such as those against free-radical damage, can be brought to bear. It is unlikely that seeds can be treated in advance of storage to prevent deterioration, although storage conditions can be devised which minimize damage (e.g. low temperatures and a dry atmosphere). But as we will consider now, maintenance for long periods in the dry state is not the natural way for many seeds to be stored. Rather, as they lie in the ground, they are intermittently to frequently wetted, and hence undergo periods of both metabolic activity and relative quiescence.

SEEDS IN THE SOIL: THE NATURAL SEED BANK

The Soil Seed Bank

Seeds buried in the soil for long periods must be able to cope with a series of problems, not least of which are the necessity to sustain themselves metabolically when hydrated and to remain in a dormant state until appropriate germination and growth conditions are available.

There is an appreciable reserve of viable seeds in the soil underlying a wide range of plant communities. The species composition of a seed bank reflects the differing strategies of past and present components of the vegetation, and a great diversity is often apparent (Roberts 1981). Studies of the litter and surface soil layers of North American forests have shown the presence of viable seeds of species not represented in the vegetation, thus indicating long-term survival of species even from previous successional stages (Livingston and Allessio 1968). An indication of the seed banks present in some western forest stands is presented in table 1. In coniferous forests there is a virtual absence of viable seeds of the dominant tree species, owing to low seed inputs and rapid losses from the surface seed bank (Kellman 1974; Whipple 1978). The predominant seeds present are those which arise after clear-felling. In the U.S.S.R. the number of viable seeds present in the soil of a 100-year-old southern tiaga forest (Picea abies and Vaccinium myrtillus) was in the order of 1200-5000 m^{-2} (Karpov 1960). But little correspondence was found between the floristic composition of the ground flora and that of the seed bank, the latter being comprised of species involved in early successional stages, or present in clearings. In old and comparatively undisturbed Picea or Picea/Pinus forests in the Moscow area (Petrov 1977) species of seeds of herbs and shrubs were present even though the vegetative stages of these species were virtually absent from the vegetation.

Table 1.--Some examples of viable seeds present in the soils of Western North American forests

Province or state	Major forest species	Age of stand (years)	Depth of burial (cm)	Seeds per m^2
British Columbia	Tsuga heterophylla	100	0-10	1016
	Pseudotsuga menziesii			
Oregon	Abies grandis	130	litter + 4	421
	Pinus contorta			
	Abies grandis	150	litter + 4	1863
	Picea engelmannii			
	Abies grandis	175	litter + 4	3447
	Larix occidentalis			
Colorado	Picea engelmannii	325	0-5	53
	Abies lasiocarpa			

Excerpted from Roberts (1981)

In northern hardwood stands the situation is somewhat different. Analysis in the spring of such stands in Pennsylvania dominated by Prunus serotina, Acer saccharum or Acer rubrum showed that they contain seeds of P. serotina, P. pensylvanica and Betula spp. in the soil (Marquis 1975)--about 370 m^{-2}. Seeds of some species (A. saccharum, Tsuga canadensis and Fagus grandiflora) germinated mainly in the first spring, and hence were only transiently present in the seed soil bank. Other species survived for up to 5 years (Fraxinus americana, P. serotina and Betula spp.), while high numbers of P. pensylvanica seeds remained viable in the soil for in excess of 30 years after this species had died out of the overstory. Evidence for even more persistent seeds in a forest understory has been presented: seeds of Comptonia peregrina have survived for 70 years or more beneath a Pinus strobus forest in Connecticut (Del Tredici 1977).

In general, though, most of the shade-tolerant true forest species do not produce seeds which enter the buried seed bank. This is also generally true for the dominant trees of mature forests. The greatest number of seeds present in the soil beneath closed forest or woodland are those of species commonly found in more open habitats such as clearings or the early stages of secondary successions. Such seeds may persist in the soil for 30 years or more.

Contrasting this situation in forest soils is that which exists in arable and grassland soils. In arable soils the average number of viable seeds at plough depth (to approx. 20 cm) usually exceeds 4000 m^{-2}, and in very weedy fields may be around 75000 m^{-2} (Jensen 1969). The main contributors to banks of arable seeds are the annual weeds, which often account for at least 95% of all seeds; those of perennial weeds and crop species are only poorly represented. Quite often there are one or two species which have seed numbers much greater than the rest.

Seed Burial and Dormancy

The probability that a seed will remain viable in the buried state is enhanced by the presence of dormancy mechanisms which delay germination in the period immediately following seedfall. Some seeds are dormant when they are shed from the mother plant, and are said to exhibit an innate or primary dormancy (Harper 1957; Bewley and Black 1982). Others acquire dormancy after shedding and are said to exhibit enforced dormancy or secondary dormancy (Harper 1957; Bewley and Black 1982). Some examples of primary dormancy are characteristic of the embryo, and include the need for an extended period of incubation in warm moist conditions to allow maturation of the embryo, inhibition of germination by light or a specific requirement for stimulation by light, or a requirement for chilling. Another type of dormancy mechanism is coat-imposed, due to some sort of mechanical restraint set up by the structures surrounding the embryo. The secondary dormancy which develops in already dispersed, mature seeds is enforced when seeds are prevented from germinating by the unfavourable conditions prevailing in the habitat in which they find themselves.

Germination of buried seeds may be held in check for many years, often until some disturbance occurs. If cultivated soil is turned over, or if a natural disturbance takes place as in a river bank, many of the buried seeds germinate and a flush of seedlings results. A major factor in the promotion of germination is light, and as little time as half a second exposure to full sunlight can cause many seeds to germinate and produce seedlings (Wesson and Wareing 1969a,b; Sauer and Struik 1964). It has been reasonably concluded, therefore, that many seeds which are light-requiring normally fail to germinate because burial in soil excludes the light. But many of the species that appear after soil disturbance are known to produce seed which, when freshly shed from the mother plant, are capable of germinating in darkness. Hence seeds of such species must acquire a light-requirement when buried (Wesson and Wareing 1968; Taylorson 1972). This is because burial induces a secondary dormancy by mechanisms which still remain to be explained. Light sensitivity may also be lost during burial, e.g. as in Barbarea vulgaris, the seeds of which are light sensitive when freshly dispersed, become insensitive to light after a period of burial, and then acquire light sensitivity once more (Taylorson 1972).

The effects of light in relation to burial might act to secure the most favourable position in the soil for germination. It would be undesirable for small seeds to commence germination at too great a depth in the soil since, because of their limited food reserves, they may be unable to grow sufficiently to reach the light and become autotrophic.

Besides absolute exposure to light, exposure to light of appropriate wavelengths is also important for germination. The spectral energy distribution of sunlight passing through a canopy of leaves is greatly reduced in the dormancy-breaking red region, and is relatively enriched in the far-red region (Holmes and McCartney 1975). Some seeds, therefore, will become dormant as a result of irradiation with canopy light and will germinate only later when a dormancy-releasing factor, such as chilling or light (usually direct sunlight) has been experienced (Fenner 1980). This mechanism explains the paucity of seedlings on forest floors and the flush that follows clearing in the leaf canopy, brought about when individual trees die and fall, or when tree removal occurs.

The second major environmental factor which promotes the germination of seeds in the soil bank is temperature. Seeds whose dormancy is broken by chilling will germinate when temperatures begin to rise in early spring, which has dual advantages. Firstly, the emergence of seedlings is prevented immediately before inhospitable winter conditions; secondly, seedlings can establish themselves prior to extensive shading by leaves. Hence species

inhabiting deciduous woodlands, including the nascent tree seedlings themselves, derive benefit by germinating before the leaf canopy appears. Germination of buried seeds in situ is often brought about by a response to diurnal fluctuations in temperature which may result from the removal of the insulating layers, such as canopy foliage, litter or humus (Grime 1979). Different sizes of gaps in the overlying cover influence the amplitude of the temperature fluctuation, which in turn appears to correlate with the germination percentages. The capacity to respond to particular amplitudes of temperature fluctuation in darkness may act as a depth-sensing mechanism, such that the dampening of the amplitude can be used by dormant seeds to determine the depth at which they are buried. Clearance of vegetation can therefore have important effects in addition to an alteration of the light environment in the top layer of the soil; thus buried seeds can use both temperature sensitivity and their phytochrome system to give them positional information (Thompson and Grime 1978).

Seeds of any species represented within a seed soil bank exhibit polymorphism with respect to their germination requirements. Seeds produced by the same population of plants (Grousiz and others 1976) or even by one individual plant (Cavers and Harper 1966) may show considerable differences in their response to environmental cues, and there may be very wide variation with respect to the amplitude of diurnal fluctuation in temperature required to initiate germination. This is of great value in environments where the risks of seedling mortality are high and synchronous germination of the seed bank could put the population in peril of extinction.

Although seeds in soil banks display polymorphism in their germination requirements, which is of considerable importance for the maintenance of their genetic diversity and for recolonization, the recurrent germination of seeds from the soil seed bank is a financially draining problem for farmers, who must combat persistent weeds like wild oats, wild mustard and redroot pigweed. Efforts have been made to "flush" the soil with promoters to induce the stored population to germinate simultaneously. Success has been very limited, although application of ethylene to the soil does break the dormancy of some buried species (Schonbeck and Egley 1981).

Seedling Banks - A Form of Persistence for Forest Species?

For many forest species the time between seed shedding and germination is relatively short (van der Pijl 1972), although among temperate forest trees it is not uncommon for germination itself (e.g. *Fagus sylvatica*) or plumule extension (e.g. *Quercus petraea*) to be temporarily delayed. Such seeds do not accumulate in persistent seed banks, however. In mature temperate forests a common regenerative strategy is for tree seedlings and saplings to persist for long periods in a stunted or etiolated condition (table 2). A small percentage survive to maturity by expanding into canopy gaps resulting from natural or man-made clearings. Many forest trees do not produce seeds each year, and the ability of seedlings to survive unfavourable conditions for long periods ensures that the potential for regeneration is maintained. One factor which may contribute to survival in the seedling state is the size of the seeds of temperate forest species (Ng 1978). They are often large in relation to seedling growth and may provide an effective nutrient source during the initial establishment in heavily shaded and/or nutrient-deficient environments (Grime and Jeffrey 1965).

Table 2.--Forest species which can regenerate by means of persistent seedlings

Species	Location of study
Hemlock (*Tsuga canadensis*)	N. America
Norway spruce (*Picea abies*)	Sweden
White oak (*Quercus alba*)	N. America
Holly (*Ilex aquifolium*)	U.K.
Sugar maple (*Acer saccharum*)	N. America
Beech (*Fagus grandiflora*)	N. America

After Grime (1979)

STORAGE IN THE IMBIBED STATE

Almost any combination of time, temperature and moisture content will result in loss of viability of dry stored seeds and will result in some genetic damage in the survivors. Increasing chromosome damage occurs with increased periods of storage, and this is manifested in an increased number of aberrant cells (Roberts 1975). While accumulation of genetic damage in stored seed lots that are planted for food or feed production may be of little consequence, unless expressed in the first generation of planting, such damage in seeds grown for germplasm stock may have more serious long-term implications. A stored seed lot with little reduction in viability could harbour a considerable number of mutations, which would not be expressed immediately in the generation grown from that seed, but which would begin to segregate in subsequent generations, and in all those thereafter.

Why aging seeds accumulate chromosome damage is not understood, but it is apparent that it can be circumvented if seeds are stored in the imbibed state. When seeds of lettuce (*Lactuca sativa*) and ash (*Fraxinus excelsior*) are maintained in a fully imbibed state, in a dormant condition, they maintain their full capacity for germination for years, and yet sustain very little chromosome damage (table 3). Loss of viability from seeds stored at low moisture content (approx. 10%) might result from inactivity of enzyme systems capable of repairing storage-induced damage to DNA, and also to other essential macromolecules (and organelles in the cytoplasm). Assuming that repair can only occur successfully in the fully imbibed state, then any damage suffered by

the wet-stored seeds will be continuously repaired and will not accumulate. In dry-stored seeds, the repair mechanisms will become activated upon imbibition after storage, but by this time the damage might be so extensive and beyond restitution that viability would be lost.

Table 3.--Effects of a six-month storage period at different water contents on the germinability and extent of chromosome damage in radicle tips of germinated lettuce seeds

% Moisture content of stored seed	% Germination	Aberrant nuclear divisions
9.7	17	45
7.0	80	17
5.1	100	10
100	100	2
Not stored	100	2

After Villiers (1974)

While storage of seeds in an imbibed state (or even intermittently imbibed) may be of advantage, it is pertinent to ask: how do such seeds maintain themselves metabolically without exhausting their energy sources? Recent work on imbibed-stored lettuce seeds (Powell, A. D. and others 1983, 1984) shows that when these are maintained in darkness at supra-optimal temperatures (25°C) they enter a condition of secondary (skoto-dormancy) dormancy from which they cannot be aroused by conventional dormancy breaking treatments (e.g. red light or gibberellic acid). This loss of response occurs over a 1-3 week period. Initially, as the seeds remain in the primary dormant condition there is an increase in oxygen consumption and protein synthesis (fig. 3A,B) revealing vigorous metabolic activity--even in seeds which have not received a germination stimulus. With entry into skotodormancy, however, metabolic rates fall precipitously, and are maintained at a low level during many months of storage (fig. 3A,B). The lowered oxygen consumption is the result of an inherent change in the respiratory mechanism within the seeds, and is not a consequence of restrictions in oxygen permeability due to changes in the surrounding seed coat (Powell, A. D. and others 1984). Even as protein synthesis

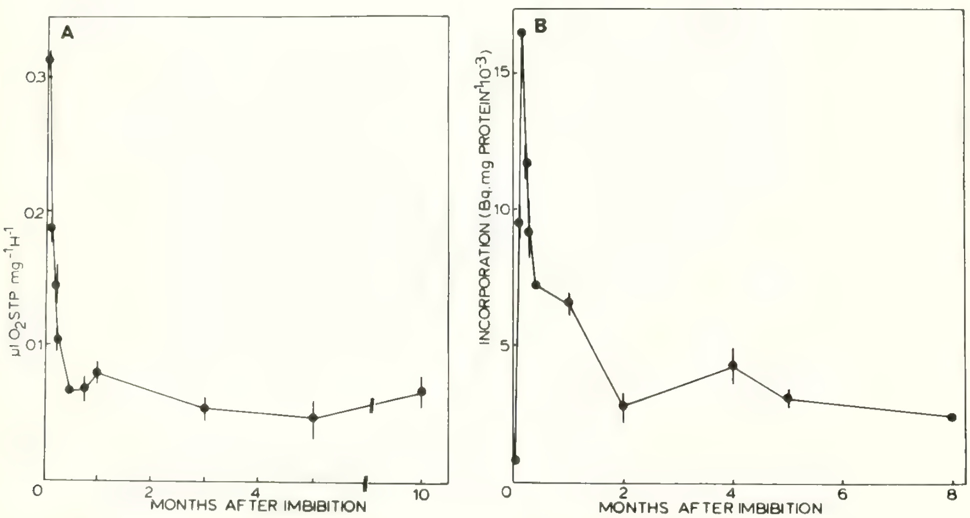

Figure 3.--Changes in (A) oxygen uptake and (B) incorporation of ^{3}H-leucine into protein by imbibed lettuce seeds stored in a dormant state for up to 10 months. After Powell and others (1983).

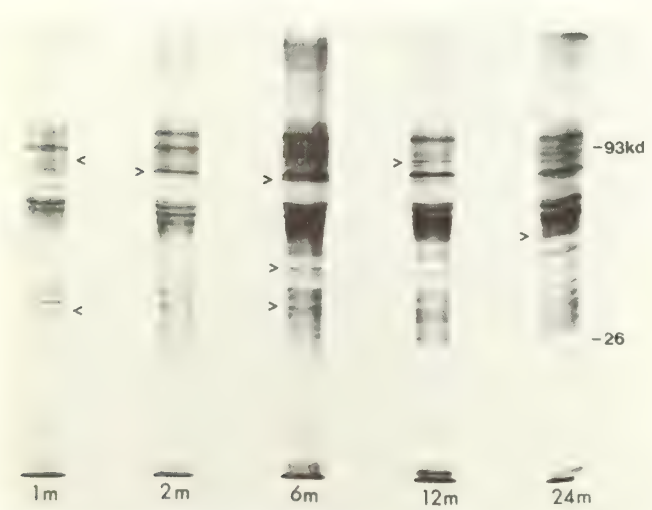

Figure 4.--Protein synthetic profiles of lettuce seeds stored imbibed in a dormant state for up to two years. Proteins were labelled with ^{3}H-leucine prior to extraction, separation by one-dimensional electrophoresis and preparation of the fluorograph. From Powell (1985).

eclines there are only a few obvious changes in he actual proteins being synthesized (fig. 4). resumably, then, the proteins required for the ormal maintenance of the cells and the etabolic "well-being" of the seeds are produced n adequate amounts.

he energy for maintenance of metabolism in the kotodormant condition probably comes from tilization of the stored reserves within the ettuce cotyledons. Mobilization is relatively low, with a decline in lipid and protein being pprox. 20% and 25%, respectively, over a en-month storage period (Powell and others 983). Extrapolating such findings to the ituation of seeds in the soil bank, it is ossible that eventually the constraint on iability could be nutritional rather than a onsequence of metabolic and/or structural eterioration. Such mobilization within seeds uried in the soil, however, would be at a much educed level compared with that in the rtificial conditions of high temperature and oisture used in the studies on lettuce seeds. eeds achieving long-term viability in the soil ould be subjected to generally lower emperatures, lower moisture contents, and ntermittent drying, all of which could prolong he time over which the storage reserves would be etained.

torage of seeds in the imbibed state may not be conomically feasible if carried out on a large cale. The seeds must be maintained under contant temperature and moisture conditions; and ontamination by fungi or other microorganisms ust be prevented. Hence, they will require ttention at regular intervals if the seed stocks re to be held in optimal conditions.

ECALCITRANT SEEDS: SPECIAL STORAGE PROBLEMS

here is a group of species that produce seeds hich normally never dry out on the mother plant; hey are shed in the moist condition and are illed if their moisture content is reduced below ome relatively high critical value. Hence these eeds do not conform to the rules which can be pplied to the orthodox group, and they have been alled recalcitrant (Roberts 1973; Roberts and ing 1980). Even when these recalcitrant seeds re stored under moist conditions their longevity ay only extend from several weeks to several onths. Included in the list of species that roduce recalcitrant seeds is a number of arge-seeded hardwoods (e.g. Corylus, Castanea, uercus, Aesculus, Salix and Juglans), aquatic pecies, and a number of important tropical lantation crops such as Coffea, Cola, Theobroma nd Hevea.

he inability to store seeds of recalcitrant pecies is a serious problem, for while vegetaive propagation is possible for some species the etention of viable seed stocks is desirable in rder to preserve maximum genetic diversity. hile dry storage is obviously out of the uestion, other methods which are suitable for rthodox seeds are also undesirable, e.g. lowemperature storage is inappropriate for seeds of tropical plants, although for those of temperate woodland species it may be of value. Even within the same genus some seeds appear to be more sensitive to low temperatures than others, e.g. Shorea ovalis seeds have to be stored above 15°C, whereas S. talura seeds can be maintained at 5°C (Sasaki 1976).

Determination of optimal storage conditions for recalcitrant seed species is generally empirical, and little has been done to define the quantitative relationship between environmental parameters and viability. Perhaps an alternative strategy for storage, other than as the seed itself is appropriate. We noted earlier that large-seeded forest species can establish themselves as stunted seedlings on the forest floor under very low light conditions. Recalcitrant seeds normally possess a rapid and uniform germination strategy, with no dormancy. The seeds are generally large. Hence it may be appropriate to store recalcitrant species as seedlings or young plants, and not as seeds. As suggested by Hawkes (1980) research on recalcitrant seeds might best be directed away from seed storage problems, and towards seedling survival at low light intensities. The most appropriate soil and moisture conditions should be elucidated, the most efficacious intensity and quality of light determined, as well as the requirement for other specific factors (e.g. mycorrhizal associations). Methods for seed storage in soil, or even in culture tubes, could be devised, and it can be reasonably expected that many seedlings could be conserved per unit area as tubes of explants. Removal of seedlings from storage, accompanied by an increase in light intensity should lead to the resumption of normal growth. Work on Cryptomeria seedlings in culture has indicated that seedlings will survive for up to two years in a healthy condition at 10°C under short-day illumination (Isikawa 1978).

SUMMARY

Methods for seed storage are many, and diverse, but for orthodox seeds storage at low temperatures (0 to -20°C) and low moisture content (5-7%) seems to be satisfactory for most species. Such conditions are not particularly "natural" as far as the seed is concerned, but it seems well adapted, both structurally and physiologically to survive them. Problems with deterioration are exacerbated by poor storage conditions, but even in the dry state seeds undergo deterioration in a manner which cannot be combatted by their natural defence mechanisms, which appear to require hydration in order to be effective. For some seeds with a low viability in storage, or a low recovery rate of metabolism upon subsequent rehydration, there may be advantages in harvesting prematurely.

Many seeds persist naturally in the soil as seed-soil banks for long periods, and therein may be in at least a partially hydrated state for extended periods. Dormancy mechanisms ensure that full germination of the seed bank does not occur, and the slow release from dormancy,

usually following an appropriate environmental due is of advantage.

Recalcitrant seeds cannot be stored in conditions of low relative humidity, and many do not withstand a low temperature treatment. Little is known about the optimum conditions required for storing such seeds, but the use of seedling banks, rather than seed banks might be most appropriate. Such seedling banks might be considered for more widespread use for conservation of difficult forest species which do not exhibit dormancy mechanisms, and which do not persist in seed-soil banks, but which can survive under sub-optimal growth conditions.

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Section 1. Cone and Seed Biology

CONE AND SEED BIOLOGY

John N. Owens

ABSTRACT: The time between cone initiation and seed maturity of conifers from the Inland Mountain West varies from 16 to 27 months. Cone and seed production are affected at many stages during these long reproductive cycles. Eight patterns of cone initiation occur which help explain how environmental factors affect cone initiation and aid in timing cone induction. Four pollination mechanisms occur. Pollination at the optimal time for each pollination mechanism can significantly increase seed set. Most pre- and post-fertilization factors affecting cone and seed development are poorly understood but can affect seed production.

INTRODUCTION

Conifer reproduction begins with the initiation of reproductive buds after a variable period of juvenile growth. The time between cone initiation and seed maturity varies from 16 to 27 months. The reproductive cycles are well known for a few conifers from the Inland Mountain West but many details are not known for most species. Generalization may be made about species within a genus but exceptions may occur. Factors can promote or reduce cone and seed production at many stages during the long reproductive cycles. Little is known about many of these factors and how they affect seed or cone development. Understanding the reproductive cycles and the factors affecting development will help increase seed production and seed quality for reforestation. The purpose of this report is to describe the status of our knowledge of cone and seed development of conifers of the Inland Mountain West, point out areas where more research is needed and suggest some new approaches which might be used to study cone and seed development.

REPRODUCTIVE CYCLES

Matthews (1963) was the first to generalize that in temperate-zone trees reproductive buds are initiated in the growing season preceding the spring in which cones or flowers appear and anthesis occurs. This generalization has held over the years with few exceptions.

Reproductive buds undergo early development before winter dormancy and overwinter at vario stages. During the second and in some species the third or fourth growing season variations occur affecting the length of the reproductive cycle. Three primary types of reproductive cycles represent the variation found in most conifers. Descriptions of many species are brief and include only a few aspects of the reproductive cycle.

The 2-Year Cycle

The most common reproductive cycle in conifers is represented in figure 1, depicting Picea glauca (Owens and Molder 1984c). Pollination occurs in the spring or early summ of the second year. The time between pollination and fertilization is brief, usuall only a few weeks. Following fertilization, embryo and seed development are rapid and continuous. Seeds are mature and may be released as early as late summer the year of pollination. Retention of seed beyond that ti is often determined by climatic or biotic requirements unique to a species and its metho of seed dispersal.

Detailed descriptions of the complete reproductive cycles of conifers with this pattern are few and include Picea (Owens and Molder 1984c), Pseudotsuga (Allen and Owens 1972; Owens 1973), Thuja (Owens and Molder 1984a) and Tsuga (Owens and Molder 1984d).

The 3-Year-Cycle--I

A second reproductive cycle is found in most species of Pinus, and several other conifers. Unfortunately, this cycle is used in general textbooks as the "typical" conifer reproductiv cycle (fig. 2). Pollination occurs in the spring or early summer of the second year, pollen tubes and ovules partially develop but then stop usually in mid-summer. Development resumes the following spring, fertilization occurs and embryos and seeds are mature in the fall. Seeds are usually shed in the year they

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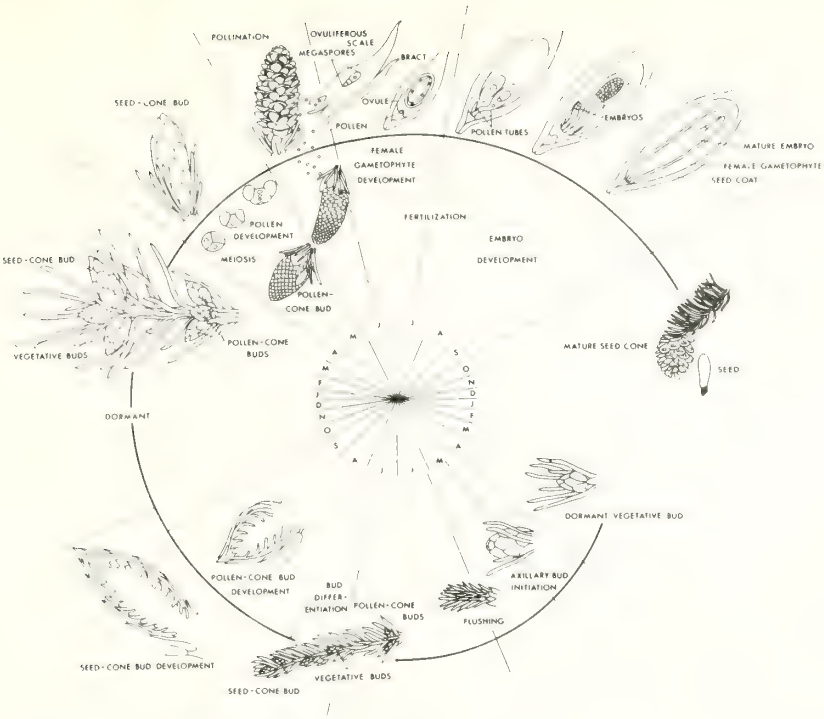
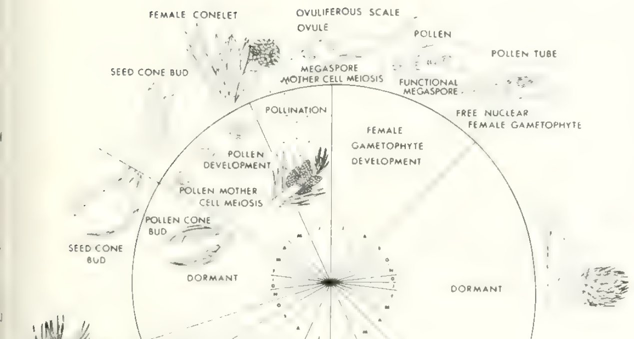


Figure 1.--The reproductive cycle of white spruce (Picea glauca) (from Owens and Molder 1984c).



igure 2.--The reproductive cycle of lodgepole ine (Pinus contorta) (from Owens and Molder 984b).

ature. Serotinous seed cones may remain closed or many years before opening, commonly in esponse to extreme heat from fires, releasing any years of accumulated seeds at one time. his is a minimum 3-year cycle (commonly about 7 months) from reproductive-bud initiation to eed maturity. Complete descriptions of this ype of reproductive cycle are limited to Pinus Lill 1974; Owens and Molder 1984b). Similar ife cycles are shared by a few other conifers from the northern hemisphere (e.g. Sequoia) and several from the southern hemisphere (e.g. Araucaria, Podocarpus) (Singh 1978).

The 3-Year-Cycle--II

A third reproductive cycle is found in a few conifers in the Cupressaceae. Pollination occurs in the spring or early summer of the second year, and fertilization occurs within a few weeks. Embryo and seed development begin but become arrested in late summer or fall. The seeds and cones overwinter in a dormant condition, then resume development in the spring of the third year (fig. 3). This reproductive cycle has been completely described for Chamaecyparis nootkatenis (Owens and Molder 1984a) and partially described for several species of Juniperus (Johansen 1950).

Variations of the Basic Cycles

General silvics (Fowells 1965) and seed manuals (Schopmeyer 1974) refer to the time between pollination and seed release. However, where this time extends over more than one year the reason is not given and it is usually uncertain if the extended cycle results from the second or third type of life cycle.

A combination of the two 3-year reproductive cycles occurs in Juniperus communis (Ottley 1909; Kötter 1931) and three species of Pinus (P. pinea, P. leiphylla and P. torreyiana) (Dallimore and Jackson 1966; Francini 1958). In J. communis cone initiation occurs before winter dormancy and pollination occurs the following

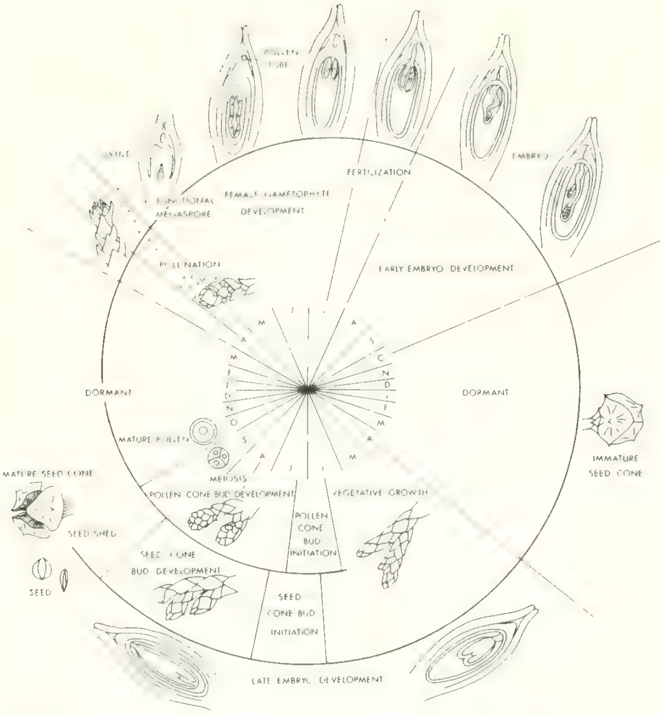


Figure 3.--The reproductive cycle of yellow cedar (Chamaecyparis nootkatensis) (from Owens and Molder 1984a).

spring. Pollen tube growth and ovule development become arrested and overwinter, with fertilization occurring in the third year. The immature embryos overwinter, then complete development during the fourth growing season. In the three species of pine, pollination occurs in the spring but pollen tube and ovule development remain arrested for two years. Fertilization, and embryo and seed maturation, occur in the fourth year.

In the long reproductive cycles there is tremendous scope for variation in the phenology, even though the sequence will remain unchanged. We must not assume that a species fits the textbook example, especially if we are attempting to control seed production. Also, as the length of the reproductive cycle increases so does the possibility of something going wrong. Therefore, it is not surprising that many species have rather low seed yields. To determine the causes of poor seed yield we must determine what went wrong at what stage of development.

CONE INITIATION

The time of cone initiation in the life of a tree and during the growing season may vary from one species to another as may the sites of cone buds in the crown and on the shoot. Understanding those variations is a prerequisite to understanding factors which affect cone initiation and for cone induction.

Cone buds are borne terminally or laterally (in axils of leaves) on the branch, and, except for the Cupressaceae, they are enclosed by bud scales. As a conifer reaches reproductive age seed cones are produced first, usually on vigorous lower order shoots, followed by pollen cones, usually on less-vigorous higher order shoots. There are several reviews of times and methods of cone initiation (Owens 1973, 1980; Puritch 1972; Owens and Molder 1977, 1979; Eis and Craigdallie 1981). Figure 4 is a summary of the most recent information. Several species from the Inland Mountain West have been studied and times and patterns within genera are usually similar.

Abies (true firs)

Several species have been studied including: A. amabilis (Ritchie 1966; Owens and Molder 1977a); A. balsamea (Powell 1974, 1977a, b); A. grandis (Owens 1984b); A. lasiocarpa (Owens and Singh 1982) and A. procera (Ritchie 1966). A summary is given by Owens and Molder (1985). Potential seed-cone buds are initiated in the axils of leaves on the upper surface of elongating primary or secondary shoots in the upper few whorls of the crown. Seed-cone buds occur most frequently on vigorous nodal shoots or on less-vigorous internodal shoots. Potential pollen-cone buds are initiated in the axils of leaves on the lower surface of elongating shoots in the mid- and lower regions of the crown. There is usually little overlap between seed-cone and pollen-cone bearing regions and seldom do the two types of cones occur on a branch. All axillary buds are initiated during early shoot elongation, at about the time of vegetative bud flush. Axillary buds do not become determined as pollen-cone, seed-cone or vegetative buds until the end of bud-scale initiation (fig. 5). Microsporophylls, bracts, ovuliferous scales,

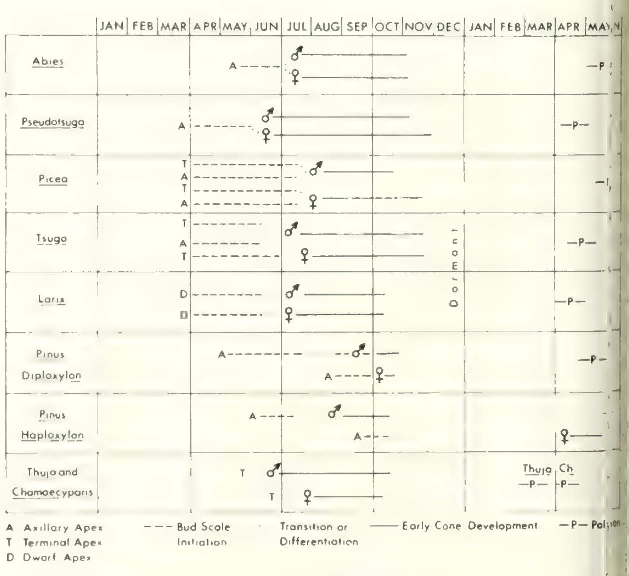


Figure 4.--Times and methods of cone initiation.

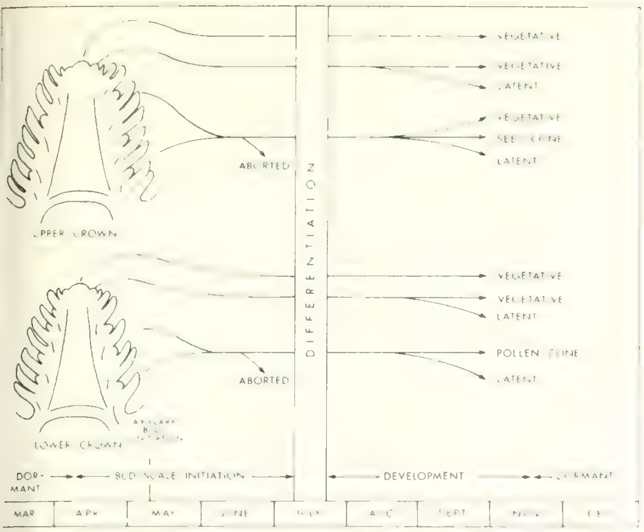


Figure 5.--Potential pathways of terminal and axillary bud development in Abies. Lower line shows vegetative bud development (from Owens and Molder 1985).

and leaves begin to be initiated about mid-July. Pollen-cone buds complete development in about 2 months, whereas seed-cone and vegetative buds continue development into autumn. All microsporophylls, bracts, fertile ovuliferous scales and leaves are initiated before winter dormancy (fig. 4). In addition to the above three alternative pathways of bud development, axillary buds may abort during early development or become latent before becoming determined (fig. 5). Aborted buds often degenerate before forming many bud-scales, whereas latent buds initiate many bud scales and retain a living apical meristem capable of future growth.

Pseudotsuga (Douglas-fir)

Douglas-fir has been studied extensively (Owens 1969; Allen and Owens 1972). It is similar to Abies in most respects, except the position of cone buds is less rigorous. There is considerable overlap of seed-cone and pollen-cone bearing regions within the crown and both types of cone buds often occur on the same shoot. In the latter case, seed-cone buds are more distal. Both cone-bud types occur primarily on the lateral and lower surfaces of shoots. All axillary buds are initiated at the onset of vegetative bud growth and have initiated several bud scales before vegetative bud flush. The earliest stages of axillary bud determination can be recognized by using histochemical tests in early June (Owens 1969). All axillary buds become anatomically determined at the same time early in July, when lateral shoot elongation is nearly complete (Owens and others 1985). Microsporophylls, bracts and leaves begin to be initiated in early July. Pollen-cone buds complete development by late summer and become dormant early in the fall. Seed-cone and vegetative buds become dormant

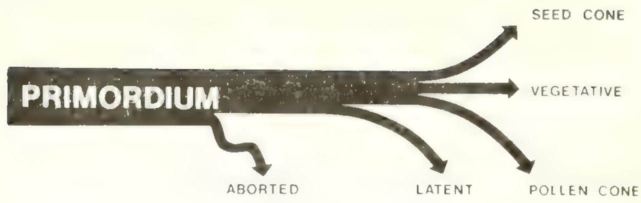


Figure 6.--Alternative pathways of axillary bud development in Douglas-fir (from Allen and Owens 1972).

late in the fall (fig. 4). All microsporophylls, microsporangia, bracts, fertile ovuliferous scales, and leaves are initiated before buds become dormant. As in Abies, terminal buds rarely become reproductive and axillary buds may abort or become latent. In Pseudotsuga the number of cone buds which develop is determined not by the number of axillary buds initiated (although this does vary) but primarily by the proportion of these buds which differentiate into cone buds (fig. 6) (Owens 1969).

Picea (spruces)

The time and method of cone initiation has been determined for P. glauca (Fraser 1962; Eis 1967; Owens and Molder 1977e), P. engelmannii (Harrison and Owens 1983), P. mariana (Fraser 1966; G. Caron, personal communication) and P. sitchensis (Owens and Molder 1976) and is summarized by Owens and Molder (1984c). Spruce cone buds may develop from terminal apices which have been vegetative for one or more years or from newly-initiated axillary apices on elongating shoots (fig. 7). Except for the presence of terminal cones, cone distribution in the crown and on branches is similar to that described above for Pseudotsuga. In Picea engelmannii when cone buds are abundant, they occur mostly in the axillary but also in the terminal position. When cone buds are few (less than 35 percent of total buds) they are about equally distributed in terminal and axillary positions (Harrison and Owens 1983). This also appears to be true for P. glauca (Owens and Molder 1977e) and P. mariana (G. Caron, personal communication).

The time of cone-bud determination is remarkably similar for most species of Picea which have been studied. Cone buds become anatomically determined at the end of bud-scale initiation which occurs near the end of the period of lateral shoot elongation (Owens and others 1977; Owens and Molder 1977e; Harrison and Owens 1983; Dunberg 1979). Dunberg (1979) stressed that biochemical differentiation must occur before shoot elongation stops and anatomical differentiation begins. Pollen-cone, seed-cone and vegetative buds in terminal and axillary positions become determined at essentially the same time in all regions of the crown of a tree.

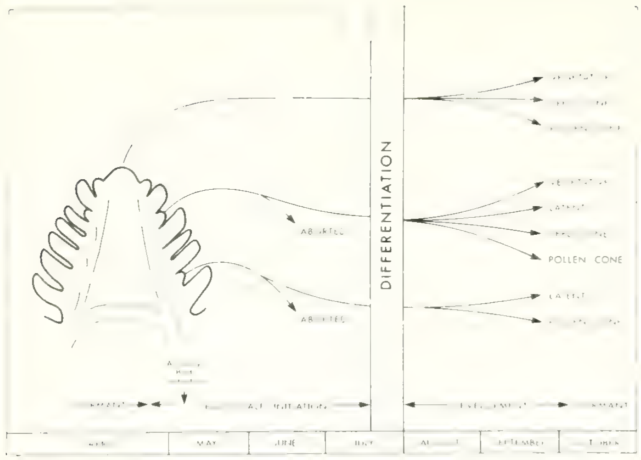


Figure 7.--Potential pathways of terminal and axillary bud development in Picea. Lower line shows vegetative bud development (from Owens and Molder 1984c).

In P. sitchensis (Owens and Molder 1976) and P. glauca growing at low elevations (Fraser 1958; Owens and Molder 1976, 1977e), bud determination begins about mid-July. In P. engelmannii growing at higher elevations determination begins in mid- to late July (Harrison and Owens 1983). The time of cone-bud determination within a species may vary with elevation and latitude, therefore provenance differences may be significant. Pollen-cone development is completed first, usually by late-September or early-October. Seed-cone and vegetative bud development may continue until mid-October in interior species (Owens and Molder 1977e; Harrison and Owens 1983) (fig. 4). All microsporophylls and microsporangia, bracts and functional ovuliferous scales, and leaves are initiated before buds become dormant (Owens and Molder 1984c). Axillary buds have the same potential pathways as in Pseudotsuga (fig. 6) and the abundance of cone buds is determined more by the pathways along which buds develop than by the number of axillary buds initiated. Terminal cone buds halt the future growth of a shoot and abundant terminal cones can reduce the cone-bud production and crown expansion of a tree.

Tsuga (hemlocks)

Only T. heterophylla (Owens and Molder 1974a) and T. mertensiana (Owens 1984a) have been studied and these are summarized by Owens and Molder (1984d). There is considerable overlap of seed- and pollen-cone buds in the crown and on branches. Seed-cone buds are terminal (some exceptions occur during cone-induction) and develop from apices which have been vegetative for 1 or more years. They form on vigorous lateral shoots in distal portions of branches. Pollen-cone buds usually develop from newly-initiated axillary buds on short lateral shoots in proximal portions of branches. They commonly form a cluster of buds at the base of the shoot but the terminal apex may also develop into a pollen cone. Cone position is essentially the same in both species (Owens and Molder 1984d). In coastal low elevation T. heterophylla, pollen-cone buds become determined in late June and seed-cone buds in mid-July (fig. 4). In coastal high elevation T. mertensiana, both pollen- and seed-cone buds become determined in late July (fig. 8).

Terminal, potential seed-cone apices have limited pathways of development--they may remain vegetative or differentiate into seed cone buds after bud scales are initiated. Axillary, potential pollen-cone buds may abort, become latent or differentiate into pollen-cone buds. In T. heterophylla, cone buds continue development until late fall, whereas in T. mertensiana development stops by mid- to late October. All microsporophylls and microsporangia, bracts and functional ovuliferous scales are initiated before dormancy. Prolific terminal seed-cone development is common and may limit subsequent vegetative growth of the branch.

Larix (larches)

Larix has dwarf (short) and long shoot buds. L. occidentalis (Owens and Molder 1979b) and L. laricina (Powell and others 1984) have been studied in detail and the position of cone-buds is generally considered to be similar in other species of Larix (Dallimore and Jackson 1966). Pollen- and seed-cone buds normally differentiate from vegetative terminal apices of dwarf shoots that are at least 1-year-old (fig. 9). Occasionally cone buds develop from terminal-long-shoot buds on suppressed branches. Pollen-cone buds are commonly proximal on nonvigorous, often pendant, long shoots. Seed-cone buds are commonly distal on vigorous, but only slightly pendant to upswept long

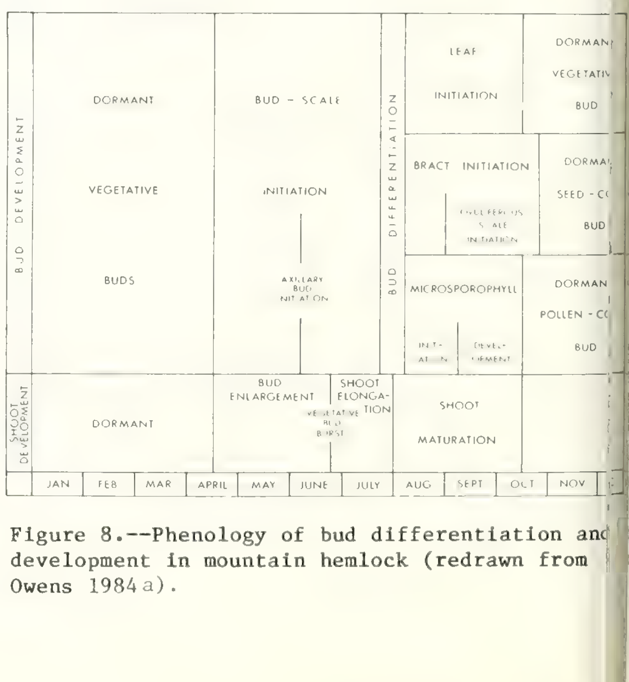


Figure 8.--Phenology of bud differentiation and development in mountain hemlock (redrawn from Owens 1984a).

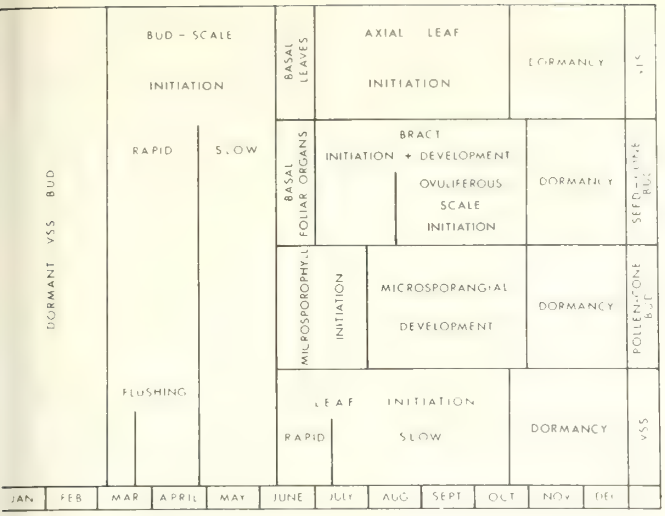


Figure 9.--Phenology of vegetative short shoot (VSS), long shoot (VLS), pollen-cone and seed-cone bud development in L. occidentalis (from Owens and Molder 1979b).

shoots. Considerable overlap occurs in distribution of cone-buds in the crown and along the branches (Owens and Molder 1979b). In L. occidentalis pollen-cone and seed-cone buds become determined in mid-June. Microsporophyll initiation is complete in about 6 weeks and is followed by microsporangial development. Bracts and ovuliferous scales are initiated until early November when both seed and pollen-cone buds become dormant (fig. 9) (Owens and Molder 1979b). Similar detailed studies have not been made for other Larix species. Related genera, Cedrus and Pseudolarix, within the Laricoideae of the Pinaceae have similar distributions of cones but details of development are not known.

Pinus (pines)

In pines, cone buds are initiated in a complex vegetative long-shoot bud (LSB) rather than on an elongating shoot or a dwarf shoot. The LSB consists of a series of scale leaves (cataphylls) which are initiated throughout the growing season. Most cataphylls have an axillary apex which initiates a series of bud scales, then differentiates into a dwarf shoot, pollen-cone or lateral LSB (fig. 10). Therefore, axillary bud initiation and differentiation occur throughout the growing season. The time when an axillary bud differentiates is determined by its position in the LSB--the proximal buds which were initiated first differentiate before the more distal axillary buds (Doak 1935; Sacher 1954; Duff and Nolan 1958; Owston 1969; Van den Berg and Lanner 1971; Sucoff 1971; Curtis and Popham 1972; Lanner and Van den Berg 1975; Owens and Molder 1975a, 1977b, c). LSB's may be monocyclic consisting of one complete sequence (fig. 10) or polycyclic consisting of two or more sequences.

Axillary buds are initiated at the base of the LSB in the spring or early summer. They initiate bud scales then differentiate into pollen-cone or dwarf-shoot buds during the summer. A more-distal group of axillary buds differentiate into dwarf shoots bearing the characteristic number of needles for the species. The most-distal axillary buds are initiated in late summer and after a period of bud-scale initiation, differentiate into either lateral long-shoot or seed-cone buds (fig. 10). In hard pine (diploxylon), lateral long-shoot and seed-cone buds differentiate in late summer or early fall in north temperate regions (Sacher 1954; Duff and Nolan 1958; Gifford and Mirov 1960; Van den Berg and Lanner 1971; Curtis and Popham 1972; Owens and Molder 1975a) (fig. 4). In soft pines (haploxylon), distal axillary primordia do not differentiate before the LSB becomes dormant. Immediately following dormancy they differentiate into either lateral LSBs or seed-cone buds (Sacher 1954; Owston 1969; Owens and Molder 1977b, c) (fig. 4).

In pines having polycyclic LSBs, more than one series of seed-cone buds may occur in a LSB but the first series usually bears most of the seed-cone buds (Lanner and Van den Berg 1975; Owens and Molder 1975a; Sweet 1979; Greenwood 1980). Polycyclic LSBs occur in many hard pines and are most common in those from southern latitudes. They have not been reported in soft pines.

Cupressaceae (cypress family)

The time and method of cone initiation has been determined only for Cupressus arizonica (Owens and Pharis 1967), Thuja plicata (Owens and Pharis 1971) and Chamaecyparis nootkatensis (Owens and Molder 1974b, 1984b). In the

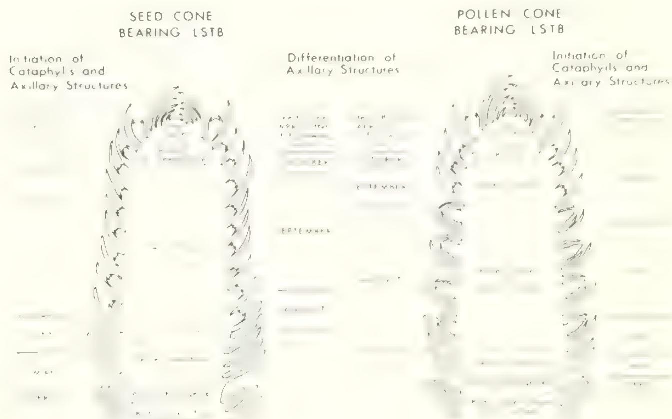


Figure 10.--The development of monocyclic LSBs of P. monticola. The columns on the left and right indicate the time of initiation and proportion of cataphylls and axillary structures initiated during this time. The center columns indicate the approximate times of differentiation of the axillary structures on each LSTB (from Owens and Molder 1977b).

Cupressaceae, cone buds form by the transition of a vegetative apex into a reproductive apex. Buds are not enclosed by bud scales. Seed cones are terminal on short lateral shoots located on distal portions of vigorous shoots. Pollen cones are terminal on proximal, less-vigorous lateral shoots. There is considerable overlap in cone distribution on branches and in the crown. Shoot elongation and leaf and axillary bud initiation occur over most of the growing season. Transition from a vegetative to a pollen-cone apex begins in early June in T. plicata, and in late June in C. nootkatensis. Transition to seed-cone apices follows in 4 weeks and 1 week, respectively (Owens and Pharis 1971; Owens and Molder 1974b, 1984a) (fig. 4). Only pollen cone initiation as a result of gibberellin A_3 treatments, rather than under natural conditions, was studied in Cupressus arizonica (Owens and Pharis 1967). In the Cupressaceae which have been studied, all microsporophylls and microsporangia, bract-scales and ovules are initiated before cone-buds become dormant in the fall.

FACTORS AFFECTING CONE INITIATION

Knowledge of time and method of cone initiation is useful in interpreting environmental or developmental factors which may affect floral initiation and in determining the correct time to attempt cone enhancement or induction.

Many studies have tried to demonstrate a relationship between environmental factors and cone initiation in regions, stands and individual trees (see reviews by Mathews 1963; Jackson and Sweet 1972; Puritch 1972; Lee 1979; Owens and Blake 1985). Correlation between seed crop and weather data are tempting. However, Rehfeldt and others (1971) cautioned that, "In any attempt to correlate previous cone crops and previous weather, problems arising from intercorrelations among the dependent and independent variables will be encountered; it is difficult to identify causal mechanism because of these intercorrelations."

Despite the problems, several factors have been identified. The very old concept that high summer temperatures favor increased floral initiation has been demonstrated in several conifer genera which grow in the Inland Mountain West, including Pinus (Maguire 1956; Daubenmire 1960), Pseudotsuga (Lowry 1966; Van Vredenburch and La Bastide 1969; Eis 1973), Abies (Eis 1973), Picea (Fraser 1958) and Larix (Yanagihara and others 1960). Increased light intensity through thinning has enhanced cone production in Pinus ponderosa (Barnes 1969) and Pseudotsuga (Reukema 1961). Photoperiod may effect sexuality of cones in P. contorta (Longman 1961), Tsuga heterophylla (Owens and Molder 1974a), Chamaecyparis nootkatensis (Owens and Molder 1974b) and Thuja plicata (Pharis and Morf 1967). Studies of moisture have given conflicting results primarily because times of cone-bud differentiation were not known. Generally moisture stress has enhanced seed cone initiation in Pinus monticola (Rehfeldt and others 1971), Pseudotsuga (Eis 1973; Lowry 1966), Abies grandis (Eis 1973) and Picea glauca (Fraser 1958). Frost resulting in lesions and girdling has increased cone production in Pseudotsuga (Ebell 1971).

The lack of positive correlations with environmental factors may result from endogenous factors within the trees. Cone-bud differentiation occurs during shoot elongation and maturation of subtending cones (Allen and Owens 1972; Owens 1984b) which are strong metabolic sinks (Ching and Ching 1962). No matter how favorable environmental factors might be, they rarely override the effects of bearing a heavy cone crop and consecutive heavy cone crops do not occur. Bumper crops may occur when endogenous and favorable environmental factors are in phase.

CONE INDUCTION

Cone induction in juvenile or otherwise non-reproductive conifers is a valuable tool in genetic tree improvement programs and in seed production for reforestation. Successful treatments are numerous and results variable depending upon the species, growing conditions and time of treatment. Any cone induction treatment must be applied before the time of anatomical differentiation of buds (fig. 4). How long before and for what duration are unknown for most species.

Various cultural treatments have been reviewed by Puritch (1972), Jackson and Sweet (1972), Brazeau and Veilleux (1976), Lee (1979) and Owens and Blake (1985). Successful treatments of genera from our region include: (1) fertilizers in hard pines (Lee 1979), soft pines (Schubert 1956; Barnes and Bingham 1963), Pseudotsuga (Ebell and McMullan 1970; Ebell 1972a, b) and Picea (Holst 1971); (2) girdling, banding and strangulation in Pseudotsuga (Ebell 1971) and Larix (Melchior 1960, 1961a, b); (3) moisture stress, usually applied by root pruning, in Pinus (Stephens 1961, 1964), Pseudotsuga (Melchior 1968; Ross and others 1985), Larix (Heitmuller and Melchior 1960) or withholding water in potted trees of Tsuga, Picea and Pseudotsuga; (4) growth of seedlings under continuous light to reduce the age to flowering in Picea (Young and Hanover 1976) and Pinus (Wheeler and others 1982); (5) altered photoperiod which may affect sexuality of cones in Pinus (Longman 1961), Picea (Durzan and Cambell 1979), Larix (Yokoyama and Asakawa 1973), Thuja (Owens and Pharis 1971) and Chamaecyparis (Owens and Molder 1977f); and, (6) shoot pruning in Pinus (Coffen and Bordelon 1981) and Pseudotsuga (Copes 1973). Many of these cultural treatments are most successful when used in conjunction with growth regulators.

About 100 research papers describe results utilizing a variety of species, growth regulators, concentrations of growth regulators

times and methods of application plus several adjunct treatments. These are reviewed or tabulated by Owens and Blake (1985). The most successful treatments have used gibberellins (GAs). GA_3 was first shown to induce cones in some members of the Cupressaceae and Taxodiaceae in the late 1950's (Kato and others 1959). Since then 19 species in 10 genera within these families have responded positively to GA_3 treatments (Owens and Blake 1985). More recently less-polar GAs, usually a mixture of $GA_{4/7}$, have induced cones in 17 species of the Pinaceae representing five genera (Larix, Picea, Pinus, Pseudotsuga and Tsuga) (Owens and Blake 1985). Best results have been achieved when $GA_{4/7}$ was applied with some adjunct cultural treatment. Progress has been slower in the Pinaceae because: less-polar GAs are not as available and are more expensive than GA_3; treatments are not as easily applied (foliar sprays may not be effective); the timing of treatment is more critical since it must correlate with stages of bud development; the length of treatment may be longer (commonly 6 weeks or more); adjunct treatments are often necessary; and sexuality of cones is not easily manipulated. Much more research is needed on all of these problems in many species. Recent research on containerized (potted) rooted cuttings, grafts and seedlings (S.D. Ross, personal communication) shows promise for the development of containerized seed orchards of some species. Basic research on the mode of action of GAs must continue if cost-effective treatments are to be developed.

Most cone induction researchers are confident that seeds resulting from induced cones are comparable in quality to those from noninduced trees because cone induction treatments are of short duration and precede seed maturation by one or more years. However, excessive flowering can result in ovule, seed and cone abortion and perhaps seed of poor quality due to competition for resources. This may be especially true in small trees but may be most easily overcome in containerized trees.

CONE-BUD DEVELOPMENT

Seed-Cone Development

Seed cones of most conifers are preformed within the bud and any ovuliferous scales initiated after dormancy are sterile (Owens and Blake 1985). Exceptions occur in Pinus. In hard pines, one-third to all ovuliferous scales are initiated before winter dormancy, depending upon the position of the cone-bud on the shoot (Owens and Molder 1975a). In soft pines (see fig. 4), all bracts and ovuliferous scales are initiated after winter dormancy (Owens and Molder 1977b). We know little about the effect of overwintering conditions on seed-cone buds. Seed-cone buds resume development before vegetative buds, often during harsh late winter weather conditions. Cone-bud abortion is a common but poorly documented phenomenon in some species.

Pollen-Cone Development

Pollen cones initiate all microsporangia (pollen sacs) before winter dormancy (see fig. 4). However, the stage of microsporangial development reached before dormancy varies between genera (fig. 11). Overwintering may begin when pollen cones are at the sporogenous stage in Pinus (Kupila-Ahvenniemi and others 1978; Owens and Molder 1977c; Owens and others 1981b) or at the pre-meiotic pollen mother cell (PMC) stage as in Picea and Abies (Owens and Molder 1977d, 1979a; Singh and Owens 1981a, b; Harrison and Owens 1983). In these genera, meiosis and pollen development occur after winter dormancy. Ultrastructural studies of overwintering sporogenous cells of Pinus (Kupila-Ahvenniemi and others 1978; Cecich 1984) and PMCs of Pseudotsuga (Singh and others 1983) have shown that a true dormant period does not occur, rather nuclear and cytoplasmic changes occur throughout the winter. This period is more correctly called a period of reduced activity rather than dormancy. Similar studies have not been made for Abies or Picea.

In Larix, Pseudotsuga, Thuja and Tsuga, meiosis begins in the fall, then becomes arrested when PMCs reach either the pachytene or diffuse diplotene stages of meiosis (Eriksson 1968a; Eriksson and others 1970a, b; Owens and Molder 1971a, b; Hall 1982). After dormancy meiosis is rapidly completed, followed by pollen development.

In Chamaecyparis and Juniperus, meiosis and pollen development occur before winter dormancy (Owens and Molder 1974b). Overwintering pollen cones contain mature, dry pollen. No structural changes have been observed during winter.

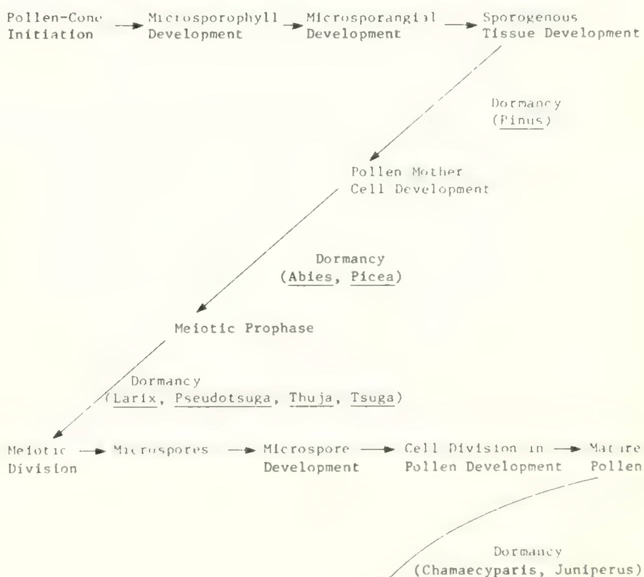


Figure 11.--Stages of pollen and pollen-cone development and times when dormancy may occur in different genera (from Owens 1982).

Winter temperatures and the stage at which pollen cones overwinter may affect pollen-cone buds and pollen quality (Eriksson and others 1970a). A higher incidence of pollen abnormalities occurred in Larix growing in Sweden, when PMC's developed beyond the diffuse stage before winter dormancy (Ekberg and others 1967; Eriksson 1968a, b). Consequently, trees moved to seed orchards in colder areas may have a higher incidence of pollen inviability or abnormalities.

Following meiosis, the tetrads of haploid microspores remain within the PMC wall for a brief time. They soon swell, burst out of the PMC wall and become suspended in fluid within the microsporangium where subsequent pollen development occurs (Singh 1978).

Two patterns of cell division occur during pollen development. In the Pinaceae (fig. 12A), prothallial cells form which have no known function. Pollen may be shed at the 4- or 5-celled stage. The body cell forms the two male gametes after pollination. Pollen is generally large, sacci (wings) are present in some genera and storage products are in the form of starch (Owens 1982; Owens and Molder 1971b, 1975b, 1977c, d, 1979a, b; Owens and others 1981b; Singh 1978; Singh and Owens 1981a, b).

In the Cupressaceae, Taxodiaceae and Taxaceae (fig. 12B), pollen has no prothallial cells and is shed at the 1- or 2-celled stage. The generative cell forms two male gametes after pollination. In these families, pollen is small, lacks sacci, is sculptured with orbicules and the storage products are oil droplets (Owens 1982; Owens and others 1980; Singh 1978).

The time sequence of meiosis and pollen development varies between species but can be separated into five stages of development: pre-meiotic division, meiotic division, microspore development, cell divisions, and anthesis. The time spent at each stage varies between species and with weather. The time from the end of pollen-cone dormancy to anthesis may be as little as 1 week in C. nootkatensis (Owens and Molder 1974b), to 12 weeks in Tsuga mertensiana (Owens and Molder 1975b). The effects of temperature on the rate of different stages of development are not known. However, increased temperatures will shorten the total time to anthesis (Sarvas 1962, 1965; Winton 1964; Boyer and Woods 1973) and forcing pollen for early pollen extraction is possible. Generally, the long period of post-meiotic pollen development makes it possible to control the rate of development in many species but the extent to which pollen can be manipulated before pollen development, vigor or viability are affected has not been determined.

POLLINATION MECHANISMS

'Pollination mechanism' is the term used to describe the process of pollen capture and entrance of pollen or pollen tubes into the ovules (Doyle 1945). The subject has been reviewed by Doyle (1945), Dogra (1964), Singh (1978), Owens (1980) and Owens and Blake (1985). All conifers are wind pollinated but differences occur in the pollination mechanisms.

Two mechanisms involving a pollination drop exist. In the Cupressaceae, Taxodiaceae and Taxaceae, ovules are flask-shaped with a narrow short neck out of which a pollination drop is exuded. The pollination drop is a clear, dilute solution of sugars (McWilliam 1958). Conelets open in the spring exposing the ovules. Within a few days pollination drops are exuded from some of the ovules at night and withdrawn during the day for 2 or 3 days. Pollination drops then remain exuded throughout the day and night for a few days. This is followed by a few days when

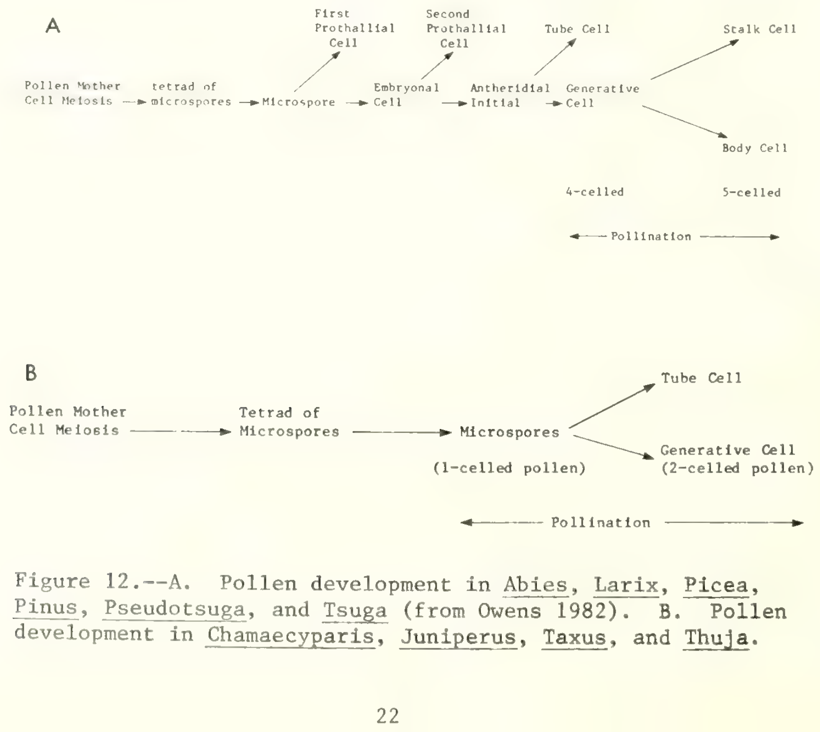


Figure 12.--A. Pollen development in Abies, Larix, Picea, Pinus, Pseudotsuga, and Tsuga (from Owens 1982). B. Pollen development in Chamaecyparis, Juniperus, Taxus, and Thuja.

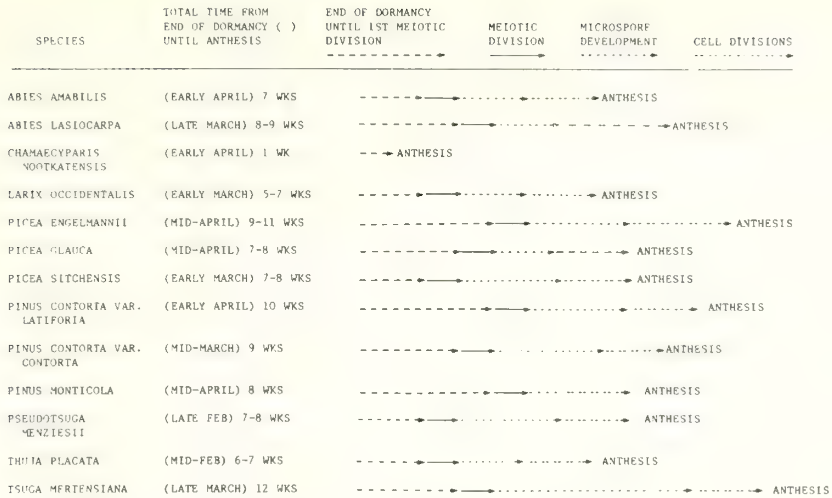


Figure 13.--Phenology of post-dormancy pollen-cone development in 13 conifers (from Owens 1982).

pollination drops are exuded only at night, then they are withdrawn permanently. Pollen landing on a pollination drop immediately sinks into the drop. Pollen adhering to the edge of the micropyle, before pollination-drop formation, is picked up by the pollination drop (Owens and others 1980).

A pollination drop is also exuded in Pinus and Picea but here the ovule is inverted and the ovule tip consists of two micropylar arms (McWilliam 1958; Lill and Sweet 1977; Owens and others 1981b; Singh and Owens 1981a; Owens and Blake 1984). The micropylar arms secrete minute sticky droplets to which pollen adheres for several days before a pollination drop forms. This provides a method by which pollen is collected and later taken in when the pollination drop floods the space between the micropylar arms (Owens and others 1981b; Owens and Blake 1984). McWilliam (1958) suggested that the pollination drop was produced by guttation but a recent study (Owens and Blake 1984) shows the drop is secreted by nectary-like tissue at the tip of the necellus.

In Abies the integument tip is funnel-shaped and lobed but no pollination drop forms (Owens and Molder 1977d; Singh and Owens 1981b). Minute droplets are secreted on the edge and inner surface of the funnel to which pollen adheres. The funnel then crimps inward carrying pollen closer to the nucellus.

Two pollination mechanisms occur in Tsuga. In the more primitive T. mertensiana, the two micropylar arms are broad flaps which secrete minute droplets to which pollen adheres. The flaps collapse, entrapping pollen grains which germinate, forming pollen tubes that grow into the micropyle (Owens and Blake 1983). In T. heterophylla, pollen has spines which adhere to long web-like cuticular hairs on the abaxial surface of the bract. After the ovuliferous-scales overgrow the bracts, the pollen grains germinate and form very long pollen tubes that grow over the bracts and into the micropyles of ovules of more distal ovuliferous-scales (Colangeli and Owens 1984).

In Pseudotsuga (Allen 1963; Ho 1980; Owens and others 1981a) and Larix (Owens and Molder 1979c; Villar and others 1984) the stigmatic tip develops into two unequal lobes covered with unicellular stigmatic hairs, and the micropyle is a narrow slit, too small for pollen to enter. Pollen sifts between the bracts of erect conelets and becomes entangled in the stigmatic hairs. This occurs for several days, then cells around the micropyle collapse and cells on the surface of the lobes elongate, carrying stigmatic hairs and attached pollen into the micropyle. Complete engulfment of stigmatic hairs occurs within about 2 weeks. There are no secretions on the stigmatic hairs and no pollination drops.

The optimal time for pollination and the duration of effective pollination vary for maximum seed yield with the pollination mechanism. In species having a pollination drop, most effective pollination occurs when the pollination drop is present (Owens and others 1981b; Owens and Blake 1984). However, in those that secrete microscopic droplets on the micropylar arms, pollen is also effectively collected on the micropylar arms. Experiments with Pinus (Owens and others 1981b) and Picea (Owens and Blake 1984) using stained pollen applied at various times show that some of this early pollen which adheres to the arms is taken into the ovule, but the most effective pollination occurs when the ovule has an exuded pollination drop. In these studies, and more recent studies of P. glauca (J.N. Owens, unpublished data), it was shown that not all ovules in a cone exude pollination drops simultaneously. Exudation occurs over several days and progresses acropetally in the cone. Therefore, different regions of each cone are most receptive at different times. This has obvious implications for controlled and

supplemental pollinations and implies that maximum seed efficiency in the field may occur when pollen arrives at the conelets over several days.

Experiments using stained pollen applied at different times throughout the receptive period show that, in Pseudotsuga, pollen is accumulated over several days and the most effective time for pollination is within about 4 days from when conelets first become receptive (Ho 1980; Owens and others 1981a). The first pollen to arrive at the stigmatic surface is taken into the ovule preferentially over pollen arriving later (Owens and Simpson 1982). In Picea glauca that was pollinated at different times with colored pollen, the pollen applied early was also most likely to be taken in and accomplish fertilization (R. Ho, personal communication).

Other pollination mechanisms which rely on a collection process (Abies and Tsuga) may have long receptive periods without optimal times. This has been demonstrated in T. heterophylla where each day for more than two weeks, previously unpollinated cones were pollinated, but the seed set was essentially the same for all dates (Colangeli and Owens 1984).

POST-POLLINATION FACTORS AFFECTING CONE AND SEED DEVELOPMENT

The time between pollination and fertilization is variable according to species (figs. 1-3). During this period seed cones rapidly enlarge and increase in dry weight (Ching and Ching 1962), ovules enlarge and female gametophytes mature (Owens and Blake 1985). After fertilization embryos and seeds develop. Both endogenous and exogenous factors may affect ovule, seed and cone development but these factors are poorly understood (Owens and Blake 1985).

Cone Abortion

Conelet abortion at and soon after pollination is common and thought to be primarily caused by low temperatures (Hard 1963; Hutchinson and Bramlett 1964; Krugman 1966), although there have been no experimental studies to prove this (Owens and Blake 1985). Death of the conelet commonly begins in the cone axis (White and Knopp 1978) and ovules, followed by wilting and browning of the bracts. Most studies of conelet loss have used Pinus, where this can usually be traced back to inadequate pollination. Sarvas (1962) estimated that 80 percent of conelet drop in P. sylvestris resulted from inadequate pollination and the remaining 20 percent resulted from damage to the conelet. He also estimated that when more than 20 percent of potentially fertile ovules aborted (due to lack of pollen) the conelet aborted. Strong clonal differences in amount and timing of conelet drop occur in Pinus (Sweet and Thulin 1969; Forbes 1971). Sweet (1973) and Owens and Blake (1985) provide complete reviews of the limited literature in this area. Generally, the physiology of conelet drop is poorly understood but the ability to induce cones on small containerized trees now makes experimental studies possible.

Post-fertilization cone loss has been reported (Brown 1970; Bramlett 1972) but is not common. Rehfeldt and others (1971) described this in P. monticola and showed it to be influenced by early summer water deficit. Sweet (1973) suggested the low cone loss at this time was due to less competition for nutrients since seeds and cones have approached full size by the time of fertilization. The seed coat is well developed at fertilization and seeds and seed wings have usually separated from the ovuliferous scales. No vascular connections exist between seed and cone at this time (Owens and others 1982; Singh and Owens 1981a, b, 1982) and seeds would no longer be strong metabolic sinks.

Prefertilization Factors Affecting Seed Development

The site and time of pollen germination vary. In Tsuga heterophylla very long pollen tubes grow into the micropyle (Colangeli and Owens 1984). In Pinus and Picea the pollination drop draws pollen to the nucellar tip where it soon germinates (Sarvas 1968; Owens and others 1981b; Owens and Blake 1984). In Abies (Owens and Molder 1977d; Singh and Owens 1981b, 1982) pollen germinates in the short micropylar canal near or on the nucellus. In Larix and Pseudotsuga, engulfed pollen elongates down the micropylar canal but a narrow pollen tube does not form until contact is made with the nucellus (Owens and Molder 1979c; Allen and Owens 1972). In all but Pinus and Picea there is considerable time between pollination and pollen germination but the stimulus for germination (or its inhibition) are not known. Many factors could prevent or retard pollen germination and pollen tube growth which would reduce seed set.

Pollen tube growth through the nucellus may take as little as one week in Pseudotsuga (J.N. Owens, unpublished data) to one year in Pinus (Sweet 1973). Competition between pollen tubes may occur during this period. The mechanisms which control pollen tube growth and penetration of the nucellus are not known. These aspects of conifer reproduction have not been studied.

Interractions may occur between pollen and pollen tubes and the nucellar and female gametophyte tissues. Such systems have been extensively studied in flowering plants but intraspecific prezygotic self-incompatability has not been reported in conifers (Hagman 1975). However, recent data shows that up to 20 percent of failure to set seed occurs before fertiization (A. Colangeli, personal communication). Pettitt (1977a, b, 1979, 1982) has detected proteins ad glycoproteins in the pollen wall of the primitive gymnosperm Cycas and has demonstrated inter-species and

inter-tissue precipitation reactions between various components of ovular tissues. This suggests that proteins could be important in prezygotic incompatability during pollen germination and pollen tube growth through the nucellus, megaspore wall and female gametophyte, all of which are genetically different from the pollen. Seriologically active substances have been demonstrated in Pinus pollen (Hagman 1975) and immunochemical differences have been detected in female gametophytes of different P. strobus trees (Eckert and Eckert 1984).

These observations indicate that prezygotic stages of development have a potentially great effect on seed set. Consequently, we have embarked on a light and electron microscopy study of pollen tube growth and interspecific pollen competition using controlled pollinations of ^{14}C labelled pollen in Tsuga heterophylla, Picea glauca and Pseudotsuga menziesii. In addition, immunocytochemical techniques are being developed to study specific proteins produced by pollen tubes in Picea.

Deficient ovules may result from ovule abortion or lack of ovule development. All cones have ovuliferous scales at the base, and to a lesser extent at the tip, which bear either no ovules or rudimentary ovules. Rudimentary ovules either do not fully develop or develop too slowly to be pollinated (Owens and others 1981a, b). This is most obvious in some species of Pinus where the majority of scales bear no fertile ovules (Sarvas 1962; Owens and others 1982). Deficient ovules also occur in fertile regions of cones but this has not been carefully studied with regard to cause or frequency within cones, trees or species. Whatever the causes, deficient ovules can significantly reduce viable seed set.

Postfertilization Factors Affecting Seed Development

The literature on conifer embryogeny is extensive and most genera have been described (Roy Chowdhury 1962; Owens and Blake 1985). Since most conifers are multiarchegoniate, more than one egg may be fertilized and resultant proembryos develop at about the same rate. Fertilization of one egg in a female gametophyte does not appear to prevent subsequent fertilization of other eggs; however, unfertilized eggs rapidly degenerate as adjacent embryos develop. The fertilization of more than one egg, simple polyembryony (SPE), is common but not universal. The resulting embryos have different genotypes. Rarely does more than one proembryo develop into an embryo.

The proembryo stage ends when suspensor cells force the apical cells into the female gametophyte. Cells of the apical tier divide and may form a single embryo or separate into four filaments, each of which may develop into a separate embryo. This is called cleavage polyembryony (CPE) and the embryos are genetically identical.

Embryo development may continue normally (figs. 1, 2), be inhibited but resume development when conditions are favorable (fig. 3), or the embryos may degenerate. Degeneration has been traced to physiological incompatability between embryos and the female gametophyte as a result of self-pollination in Pinus (Hagman and Mikkola 1963), Pseudotsuga (Orr-Ewing 1957), and Picea (Mergen and others 1965). In other conifers such as Abies (Sorensen 1982) self-pollination does not lead to embryo degeneration. It has generally been thought that selection against selfing occurs by low self-embryo viability (Sorensen 1982) and that selection occurs during the post-zygotic stages (Willson and Burley 1983). Some of these concepts may need to be re-evaluated after prezygotic stages have been thoroughly investigated.

Irregularities in embryogeny have been demonstrated (Dogra 1967; Owens and Blake 1985) but their frequency, causes and final impact on seed set are generally not known. Dogra (1967) observed that the occurrence of any one irregularity may not be common but all together they played a significat role in seed sterility. Unfortunately, large samples and numerical data are generally lacking for embryological studies. Embryo retardation and abortion are common but the causes must be studied during development rather than after seeds are mature. Classes of normal appearing seeds have been described based on the condition of female gametophyte and embryos (Dogra 1957; Owens and Blake 1985). This approach, but with emphasis on the causes, should be applied to more conifers.

Seed and Cone Maturation

Seed and cone maturation have not been thoroughly studied developmentally or physiologically. Most studies have dealt with assessing the time of cone collection which is the subject of the next session. Only a few comments relate to the present topic.

Changes within the female gametophyte and embryo during seed development have not been well described for conifers (Owens and Blake 1985). One of the most complete studies was that of Ginkgo (Favre-Duchartre 1956, 1958), a primitive gymnosperm with seeds similar to conifers. Similar but less complete studies have been made for the Pinaceae (Hakansson 1956; Takao 1960). Hakansson (1956) followed embryo development and the state of food materials in the female gametophytes of Picea and Pinus and Simola (1974) made an ultrastructural study of the embryo and female gametophytes in dry and germinating seeds of P. sylvestris. Many more complete developmental and physiological studies are needed.

SUMMARY

Cone and seed biology of conifers is a broad subject, the species are many but the researchers are few. Cones and seeds are

essential for reforestation but many factors often prevent their production. These factors are generally poorly understood. Cone and seed production can be significantly increased for many species by cone induction or enhancement treatments and improved pollination techniques. Many factors are difficult to control but warrant further study. These include factors which prevent fertilization, cause ovule and embryo retardation and abortion and cause the abortion of cones. Much of the technology is now available to significantly increase cone and seed production in many forest trees. However, further research is required to refine the technology and provide basic information about conifer reproductive development and physiology.

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IDAHO WESTERN REDCEDAR (THUJA PLICATA DONN.) CONEBEARING

STATUS IN AN UNUSUALLY DRY YEAR

William R. Gall and Allen S. Rowley

ABSTRACT: Twenty-six 1/5 acre (0.0809 hectare) plots were measured in western redcedar (Thuja plicata Donn.) stands in northern Idaho in 1979. Each plot represented one stand. Half of the plots contained western redcedar which were bearing cones of the current year, or cones that matured in 1978. The western redcedar stands bearing cones had a mean cedar d.b.h. of 11.4 inches (29 cm) versus 13 inches (33 cm) for nonbearing stands. Conebearing stands contained less basal area for the stand and western redcedar and more basal area of grand fir (Abies grandis), and western hemlock (Tsuga heterophylla). Conebearing stands had a mean elevation of 3120 feet (1125 m), and contained reproduction consisting of some combination of grand fir, western redcedar, and western hemlock; nonbearing stands were lower in elevation and had reproduction of western redcedar only and occasional Douglas-fir (Pseudotsuga menziesii).

Total height of two dominant or codominant cedars had a correlation of 0.694 with d.b.h. in conebearing stands; a larger value was found in nonbearing stands. The ratio of total height/d.b.h. had a correlation of 0.751 with the number of stems/ha and 0.751 with the number of cedar stems/ha in nonbearing stands. No significant correlation with these variables was found for conebearing stands.

INTRODUCTION

This study originated to obtain preliminary information about variation in the natural western redcedar (Thuja plicata Donn.) stands, including information about the reproductive biology of western redcedar in Idaho. Knowledge of this kind is necessary for planning a forest tree improvement program in any species or for deciding the need for a tree improvement program and to what extent the program would be worthwhile.

Currently little is known about the reproductive biology and natural variation of western redcedar in Idaho. Owens and Pharis (1971) described the phenology of western redcedar pollen and ovulate strobilus initiation, meiosis, and pollination in coastal British Columbia. Ebell and Schmidt (1964) reported on the effect of climatic conditions on western redcedar pollen release on Vancouver Island.

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MATERIALS AND METHODS

Plant Materials

Twenty-six 1/5 acre (0.0809 hectare) plots were laid out in 1979 within the natural distribution of western redcedar in Idaho. Half of the plots contained western redcedar which were bearing cones that matured in 1978 or would mature in 1979. Representative stands were chosen on relatively dry sites or moist, well-drained sites; cedar bogs were avoided. Stands with a closed canopy and of approximately 50 percent cedar at a mean d.b.h. of 12 inches (30 cm) were chosen. Diameter at breast height was measured for all trees on the plot with a diameter of 3 inches (7.6 cm) or larger. Basal area was calculated accordingly for all the trees. No increment cores were taken to provide an estimate of age.

The total height of two dominant or codominant cedar trees was recorded. The western redcedar trees were scrutinized for cones with an 8 x 2[illegible] pocket monocular.

All trees between 7.6 and 15.0 cm d.b.h. were considered to be reproduction. If any tree species or a combination of any three tree species was represented by 10 or more trees in that diameter class in a plot, that species or combination of species was considered to be reproduction.

Environmental Variables

Elevation, latitude, and longitude of each stand were obtained from either a 7 1/2' or 15' topographic quadrangle map. Aspect of each stand was observed with a hand held compass. Weather data were obtained from the National Climatic Data Center (1977, 1978, 1979).

Statistical Analysis

It was planned that data would be analyzed according to this analysis of variance:

n	Source of Variation	d.f.
2	Conebearing Status	1
13	Stands/Conebearing Status	24
t	Trees/Stands/Conebearing Status	1874
1900	Total Variation	1899

However, when analysis was begun it was observed that means for the two groups were sometimes very similar, and variation among stands within conebearing status sometimes obscured variation between the two kinds of stands. The exceptions were: percent cedar by number of stems and by basal area, total number of stems, number of cedar stems, 2-tree total height, 2-tree d.b.h. and 2-tree total height/d.b.h. A two-tailed F test (Snedecor and Cochran 1980) showed that the variance estimates for cedar basal area, plot basal area, cedar mean d.b.h., plot mean d.b.h., grand fir (Abies grandis) basal area, and western hemlock (Tsuga heterophylla) basal area were heterogenous. Therefore, it would not be appropriate to combine such variables into a single analysis as above. Instead, these variables were analyzed according to the following analysis of variance by conebearing status:

n	Source of Variation	d.f.
13	Stands	12
t	Trees/Stands	13(t-1)
	Total Variation	

Percent cedar by number of stems and by basal area were tested for skewness and kurtosis and found to be normally distributed. These two variables and total number of stems/acre and number of cedar stems/acre were analyzed according to this analysis of variance:

n	Source of Variation	d.f.
2	Conebearing Status	1
13	Stands/Conebearing	24
26	Total Variation	

Correlations were computed by conebearing status among cedar basal area, plot basal area, cedar d.b.h., plot d.b.h., number of cedar stems, total number of stems, 2-tree total height, 2-tree d.b.h., and 2-tree total height/d.b.h. Elevation was analyzed by a 2-way Chi-square test.

RESULTS

Conebearing status was found not to be independent of high and low elevation by a Chi-square test (table 1). Nonbearing stands occurred mostly at lower elevations below 3500 feet (1067 m). Conebearing stands were more variable but occurred most often at higher elevations. The stands were located from 46° 9' N to 48° 50' N and from 115° 37' W to 117° 2' W. No significant effect of the stands' location or aspect was found.

Table 1.--Number of stands in eight elevation intervals by conebearing status

Elevation Class (m)	Number of Conebearing Stands	Number of Nonbearing Stands
LOW		
457-609	0	1
610-762	0	1
762-914	3	3
914-1066	3	6
HIGH		
1067-1219	3	0
1219-1371	1	1
1372-1524	1	0
1524-1676	2	1
	13	13

[1]Chi-square = 4.25
d.f. = 1

[1]Indicates the probability of a greater Chi-square is less than 5 percent.

The field measurements define a difference in stand composition between stands bearing cones and those without cones. Table 2 displays the means of several variables for the two types of stands. The conebearing stands had less basal area for the whole stand and less western redcedar basal area. Conebearing stands did have a higher amount of basal area for grand fir, which occurred in 21 stands, 10 bearing redcedar cones. Also as seen in table 2, more basal area of western hemlock was found in conebearing stands where it existed in 12 stands, six bearing cones. Notice that the means of the two dominant tree heights were the only variables at all similar.

Table 2.--Means for selected variables by conebearing status

Variable	Conebearing	Nonbearing
Redcedar Basal area (m^2/ha)	5.16	9.99
Grand fir Basal area	3.10	1.42
Western hemlock Basal area	2.32	0.55
Total plot Basal area	10.49	13.80
Plot d.b.h. (cm)	25.9	33.0
Redcedar d.b.h.	29.0	33.0
Total height for dominant redcedar trees (m)	25.9	26.5
Stems/ha	865	919
Redcedar stems/ha	450	526

Counts of stems between 7.6 and 13.0 cm (3.0 and 5.9 inches) were used to quantify reproduction, although in shade-tolerant species d.b.h. may not be well correlated with age. Any species or combination of any three species having 10 or more stems in this d.b.h. class was arbitrarily considered to be reproducing on that plot. In some stands no stems of any species were present in this size class in sufficient numbers to qualify as reproduction. In conebearing stands reproduction consisted of cedar, grand fir, or western hemlock, singly or in a combination. In nonbearing stands reproduction consisted of cedar alone in five stands, along with Douglas-fir

(Pseudotsuga menziesii) or western larch (Larix occidentalis) in two stands.

Table 3.--Tree species of reproduction size (10 stems or more between 7.6 and 15.0 cm d.b.h.) by conebearing status of stands

Conebearing Stands		Nonbearing Stands	
Stand No.	Species Reproducing	Stand No.	Species Reproducing
9	grand fir	7	cedar
10	cedar	8	cedar
11	cedar and hemlock	16	
12	cedar and hemlock	17	cedar
13	cedar, hemlock and grand fir	18	
14	cedar and hemlock	19	cedar
15		20	cedar
22	grand fir	21	cedar and Douglas-fir
23	cedar and grand fir	24	cedar and larch
28		25	
29	cedar	26	
30		27	cedar
32	cedar and grand fir	31	

Variance estimates among conebearing and nonbearing stands were found by a two-tailed F test to be heterogenous for cedar basal area, plot basal area, cedar mean d.b.h., plot mean d.b.h., western hemlock basal area, and grand fir basal area (table 4). The variance estimates were larger in conebearing stands only for grand fir and western hemlock basal area.

Table 4.--Two-tailed F values for selected variables by conebearing status

Variable	Conebearing	Nonbearing
Plot mean d.b.h.	[1]	7.249**
Plot basal area		17.007**
Cedar mean d.b.h.		3.667*
Cedar basal area		25.165**
Stems/acre		2.098 n.s.
Cedar Stems/acre	2.236 n.s.	
Western hemlock basal area	8.589**	
Grand fir basal area	4.442**	

[1]Each F ratio is listed under the type of stand with the largest variance estimate.
**Indicates the effect was significant at P<1%.
*Indicates the effect was significant at P<5%.
n.s. Indicates the effect was not significant at P<5%.

Correlation coefficients among variables were calculated for conebearing stands and are presented in table 5. For conebearing stands the ratio two-tree mean total height/d.b.h. was not significantly correlated with any other variable. In nonbearing stands the two-tree mean total height/d.b.h. ratio was only significantly correlated (P<1%) with the number of stems/acre and number of cedar stems/acre. Two-tree mean d.b.h. was significantly correlated with plot mean d.b.h. and cedar d.b.h. (P<1%) and with plot basal area, cedar basal area and number of stems/acre (P<5%).

Variance estimates for the ratio total height/d.b.h. between conebearing and nonbearing stands were not heterogeneous by a two-tailed F test (P<5%), and the effect of conebearing status was not significant in the analysis of variance.

Relative amounts of among-stand and within-stand phenotypic variation are given in table 5 for the total height/d.b.h. ratio by conebearing status. Among-stand variation was larger than within-stand variation in both conebearing categories. These figures are based on a separate analysis of variance computed by conebearing status for the ratio of total height to d.b.h.

DISCUSSION

Conebearing stands were more common at higher elevation. Habeck (1979) reported that climax western redcedar stands in the Selway-Bitterroot Wilderness in Idaho were reproducing at higher elevations but not at lower elevations. In spite of the fact that Fowells (1965) called western redcedar a prolific seeder, Gashwiler (1969) said that seedfall of western redcedar in west central Oregon over a period of 12 years was erratic. As a possible explanation for these observations Ebell and Schmidt (1964) report a strong climatic effect on pollen production in western redcedar. For the cones observed in this study weather or elevational moisture differences could have been a factor.

The winter of 1977-78 was drier than normal. The months of January through April were 25 percent below normal for precipitation recorded at weather stations in Idaho. This time period is also a key time for western redcedar reproduction as meiosis followed by pollination is occurring (Owens and Pharis 1971). The cones we observed in 1979 were undergoing meiosis and pollination during this period. During a dry winter in 1938-39 in Illinois Martin (1952) found that the sporophylls and microsporangia of northern white cedar (Thuja occidentalis L.) became desiccated. The desiccation accounted for a low rate of survival of staminate cones. Similarly the dry winter of 1977-78 could have produced the same effect in stands we examined.

The fact that the correlation of d.b.h. and total height is different and smaller for means of conebearing than nonbearing stands suggests the two variables can be manipulated somewhat independently. Wright (1975) reported that measurements of Scotch pine (Pinus sylvestris L.) plantations in Michigan after 12 growing seasons in the field showed that there are general genes for growth rate, as well as specific genes for height and diamater growth. If improvement is to be made in the ratio total height/d.b.h., it is necessary to know if this is true for western redcedar. If d.b.h. and height can be manipulated independently

Table 5.--Correlation among plot variables for conebearing stands, 11 degrees of freedom

	2-tree mean d.b.h.	2-tree mean d.b.h./ height	plot mean d.b.h.	cedar mean d.b.h.	plot basal area	cedar basal area	total stems/ acre	cedar stems/ acre
2-tree mean height	0.694 **	0.485 n.s.	0.375 n.s.	0.526 n.s.	0.239 n.s.	0.261 n.s.	-0.376 n.s.	-0.356 n.s.
2-tree mean d.b.h.		-0.282 n.s.	0.702 **	0.825 **	0.587 *	0.623 *	-0.554 *	-0.301 n.s.
2-tree mean height/d.b.h.			-0.378 n.s.	-0.317 n.s.	-0.341 n.s.	-0.362 n.s.	0.200 n.s.	-0.059 n.s.
plot mean				0.829 **	0.784 **	0.314 n.s.	-0.866 **	-0.596 *
cedar mean d.b.h.					0.526 n.s.	0.454 n.s.	-0.860 **	-0.627 *
plot basal area						0.528 n.s.	-0.450 n.s.	-0.240 n.s.
cedar basal area							-0.027 n.s.	0.330 n.s.
total stems/acre								0.852 **

* Indicates the correlation was significant at P<5%.
** Indicates the correlation was significant at P<1%.
n.s. Indicates the correlation was not significant at P<5%.

able 6.--Relative amounts of phenotypic variation in ratio of total height to d.b.h. by conebearing status

	Among-stand variation as % of total phenotypic variation	Within-stand variation as % of total phenotypic variation
nbearing :ands	85.4	14.6
nebearing :ands	75.6	24.4

ie correlation of total number of stems and imber of cedar stems with the ratio total ight/d.b.h. in nonbearing stands may indicate an ivironmental effect of stand dynamics on that itio. The lack of such correlation in nebearing stands suggests that the number of ems cannot explain all the variation in that itio. More information is needed to separate the ivironmental factors out of the height to d.b.h. tio.

stern redcedar conebearing in closed stands in aho is not as common, especially in a dry year, as it may be in coastal forests. This variability in cone production may mean that vegetative propagation of materials obtained from ortets in natural stands is a better way of sampling genetic variation than collecting cones. If it is desired to sample genetic variation by collecting cones, it may be useful to be able to discriminate between stands that will be likely to be bearing cones and those that will not. The sample size used in the present research was not large enough to permit development of a predictive model. Use of the means reported here, however, may permit a reduction in time and travel required in locating stands bearing western redcedar cones. Further research on conebearing status of western redcedar stands would increase the sample size and permit estimation of differences between years. It might also permit development of a predictive model which would reduce the time and travel involved in finding natural western redcedar stands which are bearing cones.

If there are wet-site-adapted and dry-site-adapted genotypes of western redcedar this knowledge could be utilized in reforestation efforts. Perhaps it would be economical to plant western redcedar on drier sites than where it is climax. However, the present research cannot answer whether there are dry-site-adapted and wet-site-adapted genotypes of

western redcedar. Further research using replicated field plantations of progenies from trees on both kinds of site could be used to estimate genetic and environmental components of the difference between cedar producing cones on moist sites and cedar not producing cones on dry sites. Chemical and biochemical estimates of variability might also provide estimates of genotypic and environmental effects.

The outstanding characteristic of western redcedar is its conical shape (Anderson 1961). While a conical shope may be ideal for utility poles, it may not be the best stem form for other products. If the stem form of western redcedar could be improved, the yield of other products such as lumber might be improved. Estimates of the effect of environmental factors on the height-to-diameter ratio can be made by further research in natural stands. A possible association with age or buttressing should be investigated, and the effect of slope position and elevation should be tested. The present research has shown that number of stems per hectare and number of cedar stems per hectare were correlated with the height-to-diameter ratio in nonbearing but not in conebearing stands.

To estimate the extent to which breeding progress can be made in changing the height-to-diameter ratio, replicated plantations should be established containing progenies of trees from a number of stands. The number of trees per stand whose progenies are represented should be fairly high.

Knowledge of the site requirements for western redcedar cone production and of climatic factors affecting cone production may permit seed orchard establishment on sites where seed production can be maximized and outside pollen can be minimized. Some research needs to be done to clarify whether western redcedar seed orchards can be established on a dry site, so that irrigation can supply necessary soil moisture during each month and the seed orchard can be established some distance away from sources of western redcedar pollen. In some species, a slight drought at or before the period of cone initiation promotes the induction of large numbers of cones. Research is needed to test the effect of a slight drought on western redcedar cone initiation. Results of the present research provide some information which has a bearing on western redcedar seed orchard management and cone production. The possibility of pollen desiccation and conditions under which it may occur should also be investigated.

Research on phenology of western redcedar flower induction, flowering, and pollination in Idaho is needed to at least partially explain the results obtained in the present research, to indicate which months and what kind of weather are critical and as preparation in case any controlled pollination experiments in an outdoor breeding arboretum need to be done.

CONCLUSIONS

It was not possible in the present research to separate environmental effects from genetic ones. The objective of the present research was to obtain preliminary information about variation in and among natural western redcedar (Thuja plicata Donn.) stands, including information about the reproductive biology of western redcedar in Idah

Twenty-six stands were selected having an averag composition of approximately 50 percent cedar by number of stems or by basal area and a mean d.b. of approximately 12 inches (30 cm). Half the stands were bearing western redcedar cones; all but one were bearing the previous year cones. I general, stands selected had closed canopies and no standing water on the site.

The ratio of total height to d.b.h. of two dominant or codominant cedars did not differ significantly between the two kinds of stands. The ratio of total height/d.b.h. was significant correlated with number of stems/ha and with numb of cedar stems/ha in nonbearing stands indicatin a possible stand influence. Total height of two dominant or codominant cedars had a correlation 0.858 with d.b.h. of the same trees in nonbearin stands, but only 0.694 in conebearing stands. Both correlations were significant at the 1 percent level. These correlations, being different, suggest a possibility of d.b.h. and height having a degree of independence.

Conebearing stands had a mean elevation of 1125 m. Conebearing stands had higher basal area of grand fir and/or western hemlock. Reproducti in conebearing stands was more likely to be a combination of grand fir, western hemlock, and cedar.

Conebearing stands tended to be on high-elevatio moist sites, and nonbearing stands tended to be drier sites at lower elevation. There is some variation in the total height to d.b.h. ratio. More research will be needed to estimate environmental and genetic components of the variation in ratio of total height to d.b.h. an to estimate environmental and genetic component of the differences between conebearing and nonbearing stands, particularly with regard to the difference between stands bearing cones on mois sites and stands not bearing cones on drier site. Improvement in the conical shape of cedar is a potential. If there are dry-site-adapted genotypes of cedar, they could be utilized on a wider range of sites than those on which cedar climax. However the present research is not ab to separate environmental effects from genetic ones, which is information needed to determine wet-site or dry-site adaptations.

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EFFECTS OF COLD STRATIFICATION AND SEED COAT STERILIZATION

TREATMENTS ON PINYON (PINUS EDULIS) GERMINATION

Gerald J. Gottfried and L. J. Heidmann

ABSTRACT: One experiment compared germination capacity and energy of pinyon (Pinus edulis Engelm.) after 30- and 60-day cold stratification. Seed from five Arizona seed sources were compared. Both treatments did not affect germination capacity, but increased speed of germination. A second study evaluated the effects of six hydrogen peroxide treatments designed to improve germination and suppress mold growth during prolonged tests. Results were variable. Except for one seedlot, treatment did not improve germination capacity or energy, nor did it suppress mold. The most concentrated treatment tended to suppress germination.

INTRODUCTION

Pinyon-juniper woodlands occupy approximately 13.4 million hectares (33 million acres) in the southwestern United States. The type covers 17 percent of Arizona, mostly in the northern half, and 26 percent of New Mexico (West and others 1975) where it occurs statewide, except in the southeastern and south-central areas (Springfield 1976). The woodlands consist of pinyon (Pinus edulis Engelm.) and one or more of the following junipers: Utah juniper (Juniperus osteosperma (Torr.) Little); one-seed juniper (J. monosperma (Engelm.) Sarg.); alligator juniper (J. deppeana Steud.), and Rocky Mountain juniper (J. scopulorum Sarg.). The type is found between 1 371 and 2 438 m (4,500 and 8,000 ft) elevation; precipitation can vary from 300 to 550 mm (12 to 22 inches). It grows on a wide variety of soils and parent materials (Springfield 1976).

Management objectives for pinyon-juniper woodlands in the Southwest appear to have recently shifted towards more intensive production of wood products. Better knowledge of woodland ecology is needed to develop suitable forestry practices for these areas. Information is needed about the germination requirements of pinyon and junipers with respect to climatic factors, such as light and moisture, and physiological factors, such as seed dormancy.

The current studies concentrate on dormancy in pinyon seed. This species is of particular interest because it occurs throughout the woodland zone, and is economically important for fuelwood, especially in New Mexico, and for edible nuts. Little is known about seed dormancy of pinyon under natural conditions, or how storage will affect dormancy. Some pine species show little evidence of dormancy, while in others, up to 3 years may elapse before germination occurs (Krugman and Jenkinson 1974). Cold stratification is a common technique for breaking embryo dormancy, but its application to pinyon is poorly documented according to Krugman and Jenkinson (1974).

Understanding seed dormancy is important in research involving the effects of various environmental factors on pinyon germination and establishment. This knowledge is critical to successful growth of planting stock or for regeneration by artificial seeding. Sowing untreated seed during dormancy would lengthen the germination period, and expose seed to adverse conditions for longer periods. Seed from different locations might exhibit different degrees of dormancy and might respond differently to stratification treatments.

To solve the problem of mold in long-term germination studies, Riffle and Springfield (1968) used a 30-minute soak with 30-percent hydrogen peroxide alone, or in combination with a water soak or wash, to prevent the development of seedborne fungi. They also found that pinyon seed treated with peroxide, alone or in combination with water, germinated twice as fast as untreated seed during the first 8 days of a 28-day test period. According to Kramer and Kozlowski (1979) hydrogen peroxide stimulates seed respiration, which is essential for the early phases of germination.

The two studies reported here were designed to evaluate the effects of cold stratification and various hydrogen peroxide treatments on pinyon germination capacity and germination energy. Germination capacity is the percent of filled seeds which germinate during a period of time ending when germination is essentially complete. Germination energy is defined as the number of days necessary to achieve 50 percent germination of filled seeds. The hydrogen peroxide treatments also were evaluated for their ability to suppress mold contamination of seed during testing.

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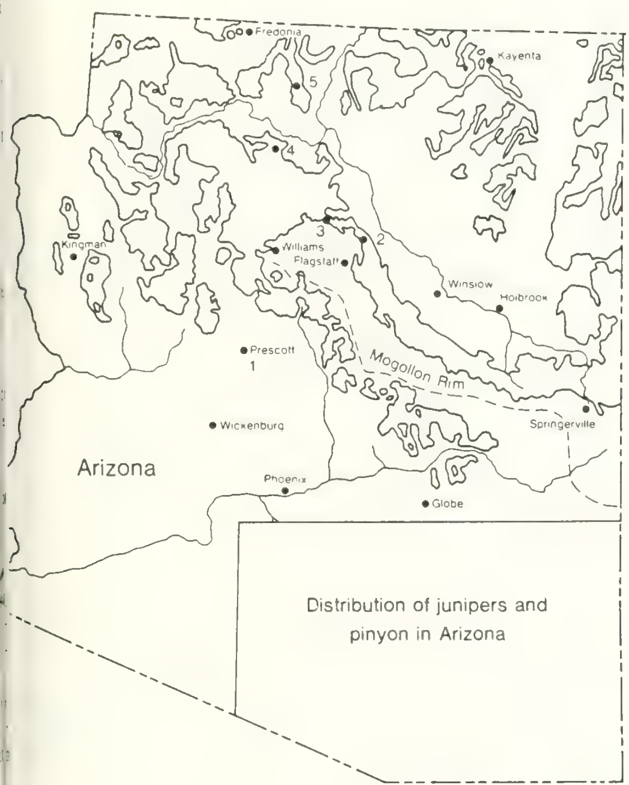
METHODS

Seed Sources

Pinyon seed was collected from five locations in central Arizona (fig. 1). Trees from the Prescott area contained both 1- and 2-needle fascicles, and have been classified as either P. edulis var. fallax or as a P. edulis x P. monophylla hybrid (Lanner 1974). Seed from Deadman Flat was collected in 1979, and from the other sources in the fall of 1983. The seed was stored at 3° C (37° F). Site characteristics of the collection areas are given in table 1; elevations were taken from U.S. Geological Survey topographic maps. Mean annual precipitation values are for the nearest weather station (Sellers and others 1985), except for Cedar Ranch, which is not near any station.



igure 1.--Map of the pinyon-juniper woodlands in rizona (Arnold and others 1964) and the location f the seedlots: (1) Prescott, (2) Deadman Flat, 3) Cedar Ranch, (4) Tusayan, and (5) North aibab.

able 1.--Characteristics of the five pinyon provenances

Location	Elevation	Pinyon height in stand	Mean annual precipitation
	- - meters - -		mm
rescott	1,689	7.3	480
eadman Flat	2,054	4.8	408
edar Ranch	2,195	12.7	--
usayan	2,091	15.1	385
. Kaibab	2,073	10.6	508

Cold Stratification Experiment

The experiment compared 30- and 60-day cold-stratification treatments with a control treatment. Seeds from each seedlot were rinsed in distilled water, then were wrapped in moistened paper towels. Wrapped seeds were put into a double plastic bag, loosely sealed, and placed in a refrigerator at 3° C (37° F). Towelling for the 60-day treatment was changed after the first 30 days. The first lot was started in March and the second in April 1984.

After stratification, 25 seeds from each of the three treatments in each seedlot were placed on glass-fiber filter paper in 10-centimeter disposable petri dishes. There were five subsamples of each seedlot-treatment combination, for a total of 75 dishes. Dishes were randomized on each of five shelves, which contained one subsample. Seeds were germinated in a Hoffman germinator programmed for 12 hours of light at 23.9° C (75° F) and 12 hours of dark at 20° C (68° F). Daytime temperature was 6.1° C (11° F), lower than recommended by the International Seed Testing Association (Krugman and Jenkinson 1974); however, preliminary tests indicated better germination at 23.9° C (75° F) than at 30° C (86° F). Although Krugman and Jenkinson (1974) recommended a schedule of 8 hours of light and 16 hours of darkness, the 12-hour interval was used, because it may better approximate conditions during the germination period, which was assumed to be summer. However, it is not known whether P. edulis germinates in the spring, summer, or during both seasons under natural conditions. The trials were not replicated in different germinators or for other time periods.

Dishes were monitored daily and were watered as necessary. Germination was recorded when the radicle equaled the length of the seed. Germinated seeds were discarded. Counts were made for 33 days until germination had essentially ended. Ungerminated seeds were cut open to determine if they were filled.

Hydrogen Peroxide Experiment

The hydrogen peroxide trial consisted of seven treatments as follows:

Treatment Number	Treatment Description	
1	Control	
2	3% H_2O_2	2½-minute soak
3		5-minute soak
4		10-minute soak
5	30% H_2O_2	2½-minute soak
6		5-minute soak
7		10-minute soak

Seeds were stirred continuously during the soaking period. Four seedlots were treated; seed from Deadman Flat was not included because of insufficient seed. Five subsamples were set up for each treatment combination. Twenty-five seeds were placed on glass-fiber filter paper in each 10-centimeter petri dish; there were 140 dishes with 28 dishes on each of five shelves. The experiment was started in January 1985.

The same germination and counting procedures used in the stratification study were followed. Counts were made for an average of 44 days. Shelf order in the germinator was rotated to avoid possible germination differences caused by microclimatic variations in the equipment. In addition, the day when mold first appeared in a dish was noted. Experience indicates that most seed becomes contaminated soon after mold is first detected.

Treatment differences in both studies were compared by one-way analysis of variance using pooled seed source as a blocking factor. Pairwise differences were calculated using Fisher's F-protected least significant difference test. One-way analysis of variance procedures were used to test for treatment differences within seedlots, and Duncan's multiple-range test was used to isolate any differences. Significance was indicated by P values at or below the 5 percent level. Germination capacity was analyzed after arc sin transformation of these data to improve variance homogeneity. Although there appeared to be differences among seedlots, they could not be evaluated statistically, because by combining the seed, spatial variability within each seed source area could not be determined. All analyses within seedlots are based on estimates of subsampling variability, not spatial variability within a seed source. A t-test was used to compare germination differences within control treatments over time.

RESULTS

Cold Stratification

Germination capacity.--The germination capacity of filled seeds was not significantly different among treatments. The averages, with standard deviations, ranged from 92.26 ± 0.05 percent for the control to 88.20 ± 0.08 percent for 30-day stratification. The range among seedlots was also small (14 percent), varying from 98 percent on the North Kaibab to 84 percent at Deadman Flat.

Germination energy.--There were differences between treatments in the number of days to reach 50 percent germination, with germination significantly faster for cold stratification treatments than for the control (table 2). Seed from the Prescott and North Kaibab showed the greatest response to cold stratification, with 50 and 82 percent decreases, respectively, in time necessary for 50 percent germination. Sixty days of cold stratification produced more rapid germination than the 30-day treatment or the control for Deadman Flat, Cedar Ranch, and Tusayan seed. However, combining the data for the five seedlots tended to reduce the difference between stratification treatments, although both were still different than the control.

The control treatments.--There appeared to be no differences in germination capacity among seedlots. Differences were apparent in germination energy. The Cedar Ranch and North Kaibab seed germinated in an average of 10.6 days, while the other three seedlots germinated in an average of 17.1 days.

Hydrogen Peroxide Treatments

Germination capacity.--Analysis of the hydrogen peroxide treatments indicated differences for the pooled seedlots (table 3). Seeds receiving the 30-percent hydrogen peroxide soak for 10 minutes germinated least (52.4 ± 25.3 percent), and significantly less than seed receiving the 3-percent solution for 5 or 10 minutes or the 30-percent solution for 2.5 minutes. These three treatments averaged 83.3 percent. The 30-percent solution for 10 minutes was similar to the control, the 3-percent for 2.5 minutes, and the 30-percent for 5-minute treatments.

Some treatment differences also were noted within three of the four seedlots (table 3). Only seeds from Cedar Ranch showed no significant difference among treatments. Germination percentages for seeds receiving the 30-percent hydrogen peroxide soak for 10 minutes were consistently lower than any other treatment within seedlots. Even the Cedar Ranch ecotype showed a slight drop of 10 percent in germination compared to the control. A drop in germination of 38 percent was noted for North Kaibab seed. The Tusayan control did not germinate well; however, the difference between the 30-percent peroxide for 10-minute treatment and the best Tusayan germination (30-percent peroxide for 2.5 minutes), which was helped by treatment, was about 46 percent.

Two of the seedlots also showed significant germination differences for the 30-percent

Table 2.--Germination energy expressed as the average number of days (with standard deviation) to achieve 50-percent germination of filled seed after cold stratification

Seedlot treatment	Prescott	Deadman Flat	Cedar Ranch	Tusayan	N. Kaibab	Total
Control	16.2±2.8 a[1]	17.6±1.5 a	10.2±0.8 a	17.6±0.9 a	11.0±0.7 a	14.5±3.6 a
30-day stratification	8.2±3.0 b	11.6±2.4 b	6.2±0.8 b	12.0±1.6 b	1.8±0.4 b	8.0±4.2 b
60-day stratification	5.6±2.1 b	9.6±0.9 c	4.4±1.1 c	8.4±2.7 c	1.8±0.4 b	6.0±3.1 b

[1]Means within each column followed by different letters are significantly different at the 5 percent level.

Table 3.--Average germination capacity (percent with standard deviation) for filled seed after hydrogen peroxide treatment

	Prescott	Cedar Ranch	Tusayan	N. Kaibab	Combined
Control	83.5± 3.7 bc[1]	94.4± 3.6 a	26.7±14.3 a	85.0± 3.9 c	72.4±30.8 ab
3% x 2.5 min	87.5±10.4 c	90.3± 3.7 a	30.3±11.7 a	89.9± 6.4 c	74.5±29.5 ab
3% x 5 min	88.7± 6.7 c	90.4±10.4 a	65.1± 9.6 b	87.9± 6.3 c	83.0±12.0 b
3% x 10 min	87.5± 3.3 c	92.8± 6.6 a	61.6±17.6 b	86.3± 5.4 c	82.0±13.9 b
30% x 2.5 min	83.5± 6.8 c	94.4± 3.6 a	69.6± 8.3 b	91.9± 3.0 c	84.8±11.2 b
30% x 5 min	69.2±16.7 ab	94.4± 4.5 a	64.8±10.4 b	70.8± 7.6 b	74.8±13.3 ab
30% x 10 min	54.2±15.2 a	84.7±10.6 a	23.2± 8.2 a	47.4±16.7 a	52.4±25.3 a

[1]Means within each column followed by different letters are significantly different at the 5 percent level.

5-minute treatment (table 3). This treatment for Prescott (69 percent germination) was statistically similar to the control and to the 30-percent 10-minute soak but less than for the other treatments, which averaged 87 percent. The 30-percent 5-minute soak for North Kaibab (71 percent) was higher than the 10-minute soak in 30-percent peroxide (47 percent) but lower than the other five treatments, which averaged 88 percent. However, the 30-percent 5-minute treatment produced relatively good germination at Tusayan.

Comparing data from the controls of the stratification and the peroxide tests indicated that Tusayan germination capacity decreased from May 1984 to January 1985. The control averaged 87 percent germination for the cold stratification test, and 27 percent for the hydrogen peroxide test. A comparison of control germination capacities for the other seedlots also showed decreased germination:

	1984	1985
Prescott	87.8	83.5
Cedar Ranch	97.5	94.4
North Kaibab	97.4	85.0

F-tests, however, indicated that only the North Kaibab seed germination capacity had also dropped significantly over the 8 months.

Germination energy.--The analysis of variance for the combined data also indicated significant differences among treatments (table 4); but the differences between treatments could not be demonstrated by the Fisher's F-protected test. It appears that seeds which received the 30-percent 10-minute soak took longer to reach 50 percent germination than it took seeds receiving the other treatments.

Comparisons within seedlots generally indicated that the 30-percent 10-minute treatments retarded germination energy, while the other treatments had no effect. Tusayan was an exception, however, exhibiting the same trend as germination capacity. The control group did very poorly, while some peroxide treatments stimulated germination. The control group never achieved 50 percent germination.

Mold.--The various peroxide treatments did not prevent or delay the contamination of seed by various seed or airborne fungi. The only significant delay--about 7 days compared to the control--was for the 30-percent 5-minute treatment of Prescott seed. There also appeared to be differences among seedlots. Cedar Ranch seed became contaminated after 23 days, while Prescott seed became contaminated in 4 days. Contamination was noted on the Prescott seed during the stratification period in the first trial. Tusayan and North Kaibab were contaminated within 10 days.

Table 4.--Germination energy expressed as the average number of days (with standard deviation) to achieve 50-percent germination of filled seed after hydrogen peroxide treatment

	Prescott	Cedar Ranch	Tusayan	N. Kaibab	Combined
Control	12.8± 1.1 a[1]	10.2±0.2 a	44.4± 2.2 a	10.2± 0.8 a	19.4±16.7 a
3% x 2.5 min	12.2± 0.4 a	10.2±0.2 a	44.4± 2.2 a	10.4± 0.5 a	19.3±16.8 a
3% x 5 min	12.0± 0.7 a	10.4±0.2 a	24.4± 5.5 b	11.2± 1.1 a	14.5± 6.6 a
3% x 10 min	12.0± 1.2 a	10.2±0.2 a	31.6±11.7 b	11.4± 1.3 a	16.3±10.2 a
30% x 2.5 min	12.4± 1.5 a	10.4±0.2 a	26.4± 5.1 b	11.0± 0.7 a	15.0± 7.6 a
30% x 5 min	20.6±15.4 a	10.4±0.2 a	29.0± 5.7 b	14.2± 3.0 a	19.3± 8.1 a
30% x 10 min	33.0±17.0 b	11.6±0.4 b	44.4± 2.2 a	31.2±14.1 b	30.0±13.6 a

[1]Number within a column followed by the same letter is not significantly different at the 5 percent level.

A sample of contaminated seeds was inspected by Dr. J. States, Biology Department, Northern Arizona University. He identified: Penicillium (2 species), yeast (3 species), Alternaria, Cladosporium, Bispora, Gliocladium, and Rhizopus. Dr. States indicates that the molds will attack and kill germinating seedlings under high moisture conditions. No effort was made to relate genera to specific hydrogen peroxide treatments.

DISCUSSION AND CONCLUSIONS

Cold Stratification

Although the germination capacity of filled seeds was not significantly different among treatments, cold stratification affected the germination energy of pinyon. Both the 30-day and 60-day treatments germinated faster than the control. Some seedlots did better after 60 days than after 30 days. Results over all seedlots, however, indicated no differences between stratification periods. While it is difficult to make recommendations after testing five seedlots, the more rapid germination of pinyon seed after cold stratification was consistent. It appears that a 30-day treatment should be sufficient for laboratory or greenhouse purposes where ideal environmental conditions are uniformly maintained. A 60-day stratification period may be more beneficial for field sowing because suboptimal conditions often occur. For example, Allen (1960) found more rapid germination of Douglas-fir (Pseudotsuga menziesii Mirb. Franco) seed following long stratification periods of up to 150 days when spring temperatures were low. Local seed should be tested to evaluate the effects of cold stratification, especially if large seeding operations are being considered.

A comparison of germination energy for the control treatments suggested differences among seedlots. The Cedar Ranch and North Kaibab seed germinated in an average of 10.6 days, 6.5 days earlier than the average for the other three seedlots.

Some combination of elevation and latitude may be responsible for the difference between the two groups. Either factor alone did not seem to influence this difference, because Cedar Ranch is south of Tusayan, while Tusayan and Deadman Flat are at a similar elevation as the North Kaibab. The growing season most likely starts later, and is shorter on more northern sites or above 2 134 m (7,000 ft). The ability to germinate quickly once proper climatic conditions are reached would give higher elevation or northern seedlings more time to become established before the onset of severe conditions, especially drought.

Hydrogen Peroxide Treatments

Although most treatments did not affect germination capacity, relative to the controls (table 3), germination capacity generally appeared lowest for seed receiving the 30-percent 10-minute treatment. Riffle and Springfield (1968), working with pinyon seed from Santa Fe, New Mexico, found that a 30-minute soak with 30-percent hydrogen peroxide treatment produced a slight but nonsignificant 18-percent increase in germination. They reported that combining water treatments with the hydrogen peroxide treatment improved germination relative to their control; but the results from all hydrogen peroxide treatments were similar.

Germination energy was generally depressed, or in the case of Tusayan, not improved by the 30-percent 10-minute treatment (table 4). Riffle and Springfield (1968), in contrast, indicated that all of their hydrogen peroxide treatments improved germination.

Ecotypic variability could account for the different results encountered in the seedlots, and for the differences with Riffle and Springfield (1968). They only tested one seed source and recognized the fact that other seedlots could react differently. The conclusions from this study also would have been different if the tests had been conducted on either Cedar Ranch or Tusayan seed alone.

Ecotypic differences also may have been a factor causing the decrease in germination capacity of the two northern seedlots (Tusayan and North Kaibab) while in storage. All attempts were made to handle all seed similarly. Meeuwig and Bassett (1983) reported that pinyon seed lost viability rapidly after 1 year; however, this may be under natural conditions. Other investigators indicated difficulties maintaining viability of singleleaf pinyon (P. monophylla) seeds under storage (Buy 1985). However, the Deadman Flat seed used in the stratification test had a germination capacity of 84 percent after 4½ years in storage. This seed was stored in a closed glass jar, while the 1983 seeds were stored in paper bags placed in loosely closed plastic bags. While this may account for better germination of Deadman Flat seed, it does not explain the differences with Cedar Ranch or Prescott seed.

The six hydrogen peroxide treatments did not prevent or delay contamination of seed by molds. Riffle and Springfield (1968) found that their treatments prevented contamination. Differences in techniques, and the longer period of treatment may account for the different results. Dishes in this study could have been recontaminated by airborne spores. However, the hydrogen peroxide did not reduce the growth of seed fungi initially present or of new contamination by airborne fungi. Riffle and Springfield (1968) also identified Penicillium, Alternaria, and Rhozopus plus Trichoderma, Cephalosporium, Aspergillus, and Fusarium. Differences in the number of days before contamination was noted and varied by seedlot, again indicating possible ecotypic variation.

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ACETONE IS UNRELIABLE AS A SOLVENT FOR INTRODUCING GROWTH REGULATORS INTO SEEDS OF SOUTHWESTERN PONDEROSA PINE (*PINUS PONDEROSA* VAR. *SCOPULORUM*)

L. J. Heidmann

ABSTRACT: Acetone is reported to be a reliable solvent for introducing plant growth regulators into various seeds without affecting germination. Several experiments in which southwestern ponderosa pine seeds were soaked in acetone for periods of 1 to 24 hours, then germinated under various temperature regimes, gave negative results even at soaking periods as short as 1 hour. Acetone is not an appropriate solvent for introducing plant growth regulators into southwestern ponderosa pine seeds.

INTRODUCTION

Germination of southwestern ponderosa pine (*Pinus ponderosa* var. *scopulorum*) is temperature-dependent (Pearson 1950; Larson 1961). Under ideal temperatures in the laboratory, 20° to 25° C (68° to 77° F), 50 percent of seeds germinate in a few days (Heidmann 1981). In the field, during the germination period, diurnal fluctuations in temperature of 4.4° to 26.7° C (40° to 88° F) are common. Under these conditions, germination may take several weeks. Cytokinin and abscisic acid (ABA) levels appear to be related to temperature changes. An increase in the level of ABA and a decrease in cytokinin have been shown during temperature stress, and are correlated with a reduction in shoot growth (Itai and others 1973). Lettuce seeds, in the dark at 35° C (95° F), were not released from dormancy by kinetin or gibberellic acid (GA_3); however, when GA_3 was supplied with kinetin, germination occurred (Khan 1975).

Dormancy in plants and seeds is likely under the control of naturally occurring hormones. According to Khan (1975), gibberellins (GAs), inhibitors such as ABA, and cytokinins have primary, preventive, and permissive roles in control of seed germination. Gibberellic acid will promote germination in the absence of ABA; but when ABA is present, GA_3 will only promote germination in the presence of cytokinin.

Heidmann (1981) showed that GA_3 and several other compounds significantly reduced the time required for 50 percent germination of southwestern ponderosa pine seeds under fluctuating temperatures similar to those encountered in the field. The compounds were applied as an aerated soak. Aeration in water alone significantly reduced the time to 50 percent germination, presumably because of the effect of oxygen. Although stimulation of germination by oxygen is a desirable trait, it masks the effect of the compounds being studied. Therefore, to eliminate the confounding effect of oxygen and to isolate the effect of the growth regulators under study, another method of introducing regulators into the seeds is required.

Tao and Khan (1974) showed that GA_3 and indole-3-acetic acid (IAA) can be introduced into the embryos of various dry seeds with acetone. Acetone itself did not adversely affect germination.

In 1983 and 1984, a series of experiments was conducted to determine the effect of acetone on the germination of southwestern ponderosa pine seeds. If acetone did not modify germination patterns, then it was to be used to introduce GA_3, ABA and N-6-benzyladenine (a cytokinin), singly and in combination, into pine seeds.

METHODS

Four experiments were conducted. The first three experiments were conducted in a similar manner. Seeds were collected on the Coconino National Forest, approximately 40 km (25 mi) north of Flagstaff, AZ, at an elevation of about 2 440 m (8,000 ft). Seeds were collected in 1979 and were stored at -17° C (2° F) until use. Viability in 1980 was 98 percent. Seeds were soaked in 100 ml of acetone for 0, 4, 8, 16, and 24 hours. After soaking, seeds were rinsed several times in distilled water, then were placed on Whatman glass fibre filter paper in 10-cm (3.9-inch) disposable petri dishes. International Seed Testing Association guidelines (1976) suggest using four replications of 100 seed for conducting germination experiments. However, because of a scarcity of seed, six replications of 50 seed were used in the first three experiments, and five replications were used in the fourth. Treatments were randomized within replications, then dishes were placed on a single shelf in a Hoffman seed germinator set, for 16-hour days and 8-hour nights. In experiment 1, day temperature was

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aintained at 27° C (80° F) and night temperature t 7° C (45° F). For experiment 2, temperatures ere 24° C (75° F) for days and 4.4° C (40° F) for ights. Temperatures for experiment 3 were 24° C 75° F) days and 18° C (65° F) nights. Temperatures hosen were those likely to be used in conducting ermination tests with plant growth regulators. esults from tests conducted at optimum temperatures ere compared to those from experiments using emperatures similar to those encountered in the ield during the germination period.

ishes were watered as necessary with distilled ater. Care was taken not to overwater, because ermination percentages of southwestern ponderosa ine seeds are lowered considerably by excess ater (Rietveld 1985). Germination counts were ade daily. Seeds with a radicle of 5 mm 0.2 inch) in length were recorded as germinated, hen were discarded.

xperiment 4 was conducted with seeds collected on he North Kaibab Ranger District of the Kaibab ational Forest, in 1962, at an elevation of pproximately 2 440 m (8,000 ft). Viability of he seed was 90 percent in 1980. The experiment as conducted in the same manner as the first hree experiments, except that seeds were soaked n acetone for 0, 1, 2, and 3 hours. For this xperiment, a Percival germinator was used. Day ength was 16 hours at 24° C (75° F), and night ength was 8 hours at 18° C (65° F).

reatment means for all experiments were analyzed sing Dunnett's T3 multiple comparison procedures or heterogeneous variance (P=0.10). Individual -tests between treatments were also run (P=0.01 nd 0.05).

RESULTS AND CONCLUSIONS

Results from the four experiments were inconsistent with wide variability. In the first three experiments, soaks in acetone of 8 hours or more generally reduced germination (table 1, P=0.1). In experiments 1 and 3, a 24-hour soak almost completely repressed germination; in the second experiment, this treatment was not significantly different from the control. Although a 4-hour soak is not significantly lower than controls, the germination is as much as 30 percent less (table 1).

Responses to germination temperatures were equally unpredictable. The first two experiments utilized minimum temperatures likely to be encountered in the field during the summer germination period. A temperature regime of 27° C (80° F) days and 7° C (45° F) nights, resulted in the highest germination percentage for the control (84 percent), while germination for the 24-hour soak was only 4 percent. Dropping the maximum and minimum temperatures 2.8° C (5° F) reduced control germination 22 percent, but resulted in a 40 percent increase in germination for seeds soaked 24 hours. In the third experiment, conducted under what are considered optimum temperatures, there was virtually no germination for the 16- and 24-hour soaking periods.

Information from the first three experiments seemed to indicate that a shorter soaking time might be desirable. This is refuted by results from experiment 4 which show that a 1-hour soak significantly reduced germination. Individual T-tests between the control and the other three treatments showed that each of the soak treatments

ble 1.--Effect of various acetone treatments on germination of southwestern ponderosa pine seeds

ak Time ours)	Experiment Number 1			2			3			4			
	Germ[1] %		Std. Dev.	Germ[1] %		Std. Dev.	Germ[1] %		Std. Dev.	Soak Time (hours)	Germ[4] %		Std. Dev.
0	84.33a[2]	a[3]	7.53	62.00a[2]	a[3]	15.65	79.67a[2]	a[3]	4.46	0	77.60a[2]	a[3]	3.85
4	69.67a	ab	27.75	58.00a	a	9.63	48.33a	a	25.91	1	46.80b	b	20.62
8	21.00b	bc	23.58	14.33c	b	12.42	8.67b	b	5.89	2	52.40a	b	22.60
16	14.67b	c	15.68	19.33bc	b	23.55	0.00c	c	0.00	3	39.60a	b	31.09
24	4.00b	c	6.20	44.33ab	a	5.57	0.33c	c	0.82				

ean of 6 replications of 50 seeds.

eans within each column followed by the same letter are not statistically different at the 0.1 level cording to Dunnett's T3 multiple comparison procedure.

eans within each column followed by the same letter are not statistically different at the 0.01 level r experiments 1, 2, and 3 or at the 0.05 level for experiment 4 according to individual T-tests between irs of treatments.

ean of 5 replications of 50 seeds.

reduced germination significantly (P=0.05). The discrepancy between Dunnett's multiple comparison procedure and individual T-tests is because Dunnett's method is based on an overall experiment-wise Type I error, and individual T-tests use a comparison-wise Type I error (King 1985).

These results confirm the erratic behavior of southwestern ponderosa pine seeds when treated with various materials. Although seeds can be treated with strong oxidizing agents, such as hydrogen peroxide, without affecting germination (Heidmann 1981), other treatments, such as a 15-second soak in sodium hypochlorite (Clorox), significantly repressed germination (Ronco 1985). It appears that acetone adversely affects the germination of ponderosa pine seeds. Soaking periods as short as 1 hour significantly repressed germination. This is contrary to findings by Tao and Khan (1974) that indicate various seeds can be soaked in acetone for as long as 28 hours without affecting germination. Milborrow (1963) soaked several species of seeds in acetone for periods as long as 3 months without deleterious effects. The primary conclusion to be drawn from these experiments is that acetone is unreliable as a solvent for introducing materials into the embryos of ponderosa pine seeds. In experiments currently in progress, growth regulators are being introduced to the embryos under vacuum.

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ARE YOU GETTING PONDEROSA PINE AND DOUGLAS-FIR

CONE CROPS AT HIGH ELEVATIONS?

Glenn L. Jacobsen

ABSTRACT: Research documentation and personal observations of cone crops at the upper elevation ranges of old-growth ponderosa pine and Douglas-fir in Central Idaho indicate a longer cone crop interval than the normal interval of 4 to 5 years for ponderosa pine. It appears that cone crops for ponderosa pine at 5,500- to 6,000-foot elevations and Douglas-fir at 6,000- to 6,500-foot elevations must coincide with a heavy to extremely heavy cone crop at lower elevations before we can obtain a collectible cone crop.

INTRODUCTION

Review of research literature for the Idaho area, Lucky Peak Nursery reports from 1965 to 1984, and observations made on the Payette and Boise National Forests in Central Idaho indicate a wide range of variability of cone crops, especially with ponderosa pine and Douglas-fir.

In Central Idaho, ponderosa pine on commercial forest land occurs between the elevations of ,000 to 6,500 feet above sea level. Douglas-fir occurs between the elevations of 3,500 to 7,000 feet. The vast majority of these species are in old growth stands that are in a static condition. Cone crop records generally indicate the lower the elevation the heavier the cone crop. Cone crops of ponderosa pine at the 5,500- to 6,000-foot elevation and Douglas-fir at the 6,000- to ,500-foot elevation have been very sparse.

The trend appears to be that whenever conditions are right for a better than average ponderosa pine cone crop, we also have at least an average Douglas-fir cone crop. This may vary by Ranger District and areas within Districts.

RESEARCH

Heavy ponderosa pine crops were documented (Curtis and Foiles 1961) in Central Idaho in the following years:

- 1936 - Heavy cone crop
- 1940 - Heavy cone crop
- 1941 - Cool moist summer--widespread establishment of seedlings
- 1958 - Extremely heavy cone crop
- 1959 - Below normal summer rainfall--poor establishment of seedlings
- 1962 - Average crop - less than 1/2 size of 1958 crop
- 1963 - Cool, moist summer months--unusually successful natural regeneration

No research data are available on cone crops from 1964 to the present time for Central Idaho.

CONE COLLECTION RECORDS

Cone collection records for the Payette National Forest indicate collectible cone crops in the following years, although most crops were light. Heavy ponderosa pine crops occurred in 1958, 1962, and 1971. Collectible crops are defined as one bushel of cones per tree.

Year	Species	Elevation range (feet)
1958	Ponderosa pine	Unknown
1962	Ponderosa pine	3,000 - 4,000
1963	Ponderosa pine	3,000 - 4,000
1964	Ponderosa pine	3,000 - 5,000
	Douglas-fir	4,000 - 6,000
1965	Ponderosa pine	3,000 - 4,000
	Douglas-fir	4,000 - 5,000
1971	Ponderosa pine	4,000 - 6,000
	Douglas-fir	5,000 - 6,000
1974	Ponderosa pine	4,000 - 5,000
	Douglas-fir	5,000 - 6,000
1975	Ponderosa pine	4,000
1978	Ponderosa pine	3,000 - 5,400
	Douglas-fir	4,000 - 6,000
1980	Douglas-fir	4,500 - 5,500
1982	Douglas-fir	4,500 - 6,000
	Ponderosa pine	4,000 - 5,500

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Note the gap in cone collection between 1965 and 1971. Cone crops, if any, were light and the Forest did not believe there was a need to collect additional seed to supplement the seed inventory during this period. The seed inventory was considered adequate for the artificial regeneration need.

OBSERVATIONS

On the Payette National Forest, ponderosa pine-Douglas-fir appears to have the following cone crop intervals:

Elevation Range	Collectible Cone Crop Interval
3,000 - 4,000	2 to 3 years
4,000 - 5,000	3 to 4 years
5,000 - 6,500	Coincides with an above average crop at the lower elevations

For ponderosa pine at 5,500 to 6,000 feet and Douglas-fir at 6,000 to 6,500 feet, it appears the cone crop must coincide with a heavy to extremely heavy cone crop at the lower elevations before we get a collectible crop at the higher elevation range of these species.

The last heavy crop in ponderosa pine was 1971. Prior to that a heavy crop occurred in 1958, a 13-year interval.

The average ponderosa pine cone crop interval documented currently is 4 to 5 years (Barrett 1979).

TRENDS

With the elevation range of ponderosa pine and Douglas-fir, the trend appears to be: At the lower elevation of a species range, cone crops are 3 to 4 times more frequent than at the higher elevation range.

This trend is supported by the reforestation personnel who have tenure on Districts of the Payette National Forest and have observed cone crops throughout the years. Tenure varies from 10 to 25 years depending on the respective District. Due to the lack of high-elevation seed in the Payette's seed inventory, emphasis has been placed on trying to collect high-elevation seed if cones are available. This trend is not documented by research to my knowledge, but many forests are reporting difficulty in obtaining high-elevation seed for different species due to infrequent cone crops. Research (USDA Forest Service 1965) has documented in Central Idaho that mature and overmature ponderosa pine growing at 5,500 feet produce lower quality seed than similar trees at 4,000 feet.

MANAGEMENT IMPLICATIONS

Cone crops are not uniform in Central Idaho, with variations occurring primarily due to elevation range, tree age and vigor, and soil type.

Schmidt and Shearer (1971) found that 24 out of 25 ponderosa pine seed that reach maturity are eaten by small forest animals. This information was determined over a 6-year period with various cone crops. This, combined with insects feeding on cones and seeds, only leaves seed available for natural regeneration during average or better cone crop years.

The silvicultural and management implications of the above observations and trends are:

1. We have less opportunities for regeneration, both natural and artificial, at the higher elevation of a species range due to longer cone crop intervals.

2. If a cone crop occurs at the higher elevation of a species range, we must not miss the opportunity to collect cones or coordinate site preparation with the crop to achieve natural regeneration.

SUMMARY

Observation and trends in Central Idaho indicate ponderosa pine and Douglas-fir cone crops at the higher elevation range of these species are infrequent. This adds considerable pressure to the timber manager to collect cones at these elevations when a collectible crop does occur plus accomplish site preparation for natural regeneration with a cone crop.

Managers in areas other than Central Idaho need to ask themselves if they are getting ponderosa and Douglas-fir cone crops at higher elevation ranges. If not, they may want to place more management emphasis on cone collection during a cone crop or site preparation for natural regeneration. Douglas-fir and ponderosa pine may not be the only species with cone crop frequency problems in the higher elevation ranges.

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SEED-DISPERSAL CHARACTERISTICS OF CONIFERS

IN THE INLAND MOUNTAIN WEST

Ward W. McCaughey, Wyman C. Schmidt, and Raymond C. Shearer

ABSTRACT: This paper summarizes seed-dispersal characteristics and factors affecting dispersal of the major conifers found throughout the Inland Mountain West. Seed dispersal of these conifers is influenced by a number of physical, climatic, and biotic factors such as seed and wing size, height of cone-bearing trees, distance from seed source, physiographic position, and wind patterns. Birds and mammals also aid in the dispersal of larger seeds, particularly those that are wingless.

INTRODUCTION

Seed-dispersal information can tell us where seed will be dispersed, how much seed can be expected, and when it can be expected. This knowledge, and an understanding of seed germination and seedling survival, provides much of the basic information needed to make valid decisions about regenerating an area. For example, the seed-dispersal characteristics of a species may indicate that adequate seed can be expected throughout an area, and that natural regeneration has a high probability of success.

Conversely, dispersal characteristics may indicate that much of the area is far too distant from a seed source and will have to be artificially regenerated.

Because natural regeneration is often very desirable and practical for many species, seed-dispersal characteristics should be considered in planning regeneration cuttings. This consideration can influence the choice of cutting system such as seed tree, shelterwood, or clearcuttings, the layout and timing of cutting, and site preparations.

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This paper aims at consolidating published and unpublished seed-dispersal information for 23 major conifer species found throughout the Inland Mountain West--that geographic area between the east slopes of the Rockies and east slopes of the Cascades and Sierras in the United States and Canada. Because seed and wing size, height of cone-bearing trees, distance from seed source, physiographic position, and wind patterns also influence seed dispersal, they are also included in this discussion.

SEED DISPERSAL CHARACTERISTICS

Throughout forests of the Inland Mountain West the typical shape of the seed-dispersal pattern for wind-dispersed seeds is a negative exponential curve. Quantity of dispersed seed decreases rapidly as distance from the windward seed source increases and then remains at a low level. The shape of the dispersal curve is much the same at the leeward side of openings, but total distance of dispersal and amount of seed at a given distance from seed source is less than that from the windward edge. Thus, there is a U-shaped distribution of seed dispersal across openings. Some exceptions to this dispersal pattern occur for wingless seeds of juniper (*Juniperus* spp.) and pinyon (*Pinus* spp.), which are dispersed by other modes such as birds, mammals, and gravity.

To provide a basis for comparing dispersal characteristics of nine species, we developed dispersal curves that best fit the variety of available data (fig. 1). Using number of seeds dispersed at the windward timber edge as a species base value, we related the number of seeds dispersed to different distances from the source as a percent of the amount at the timber edge. For species comparison purposes, we used the term "dispersal efficiency," defined as the ratio of number of seeds at the source to the quantity dispersed at a given distance from the source.

A natural logarithm model was used to develop curves for each of the nine species; therefore, curve shapes were similar. However, there were substantial differences in the percent of

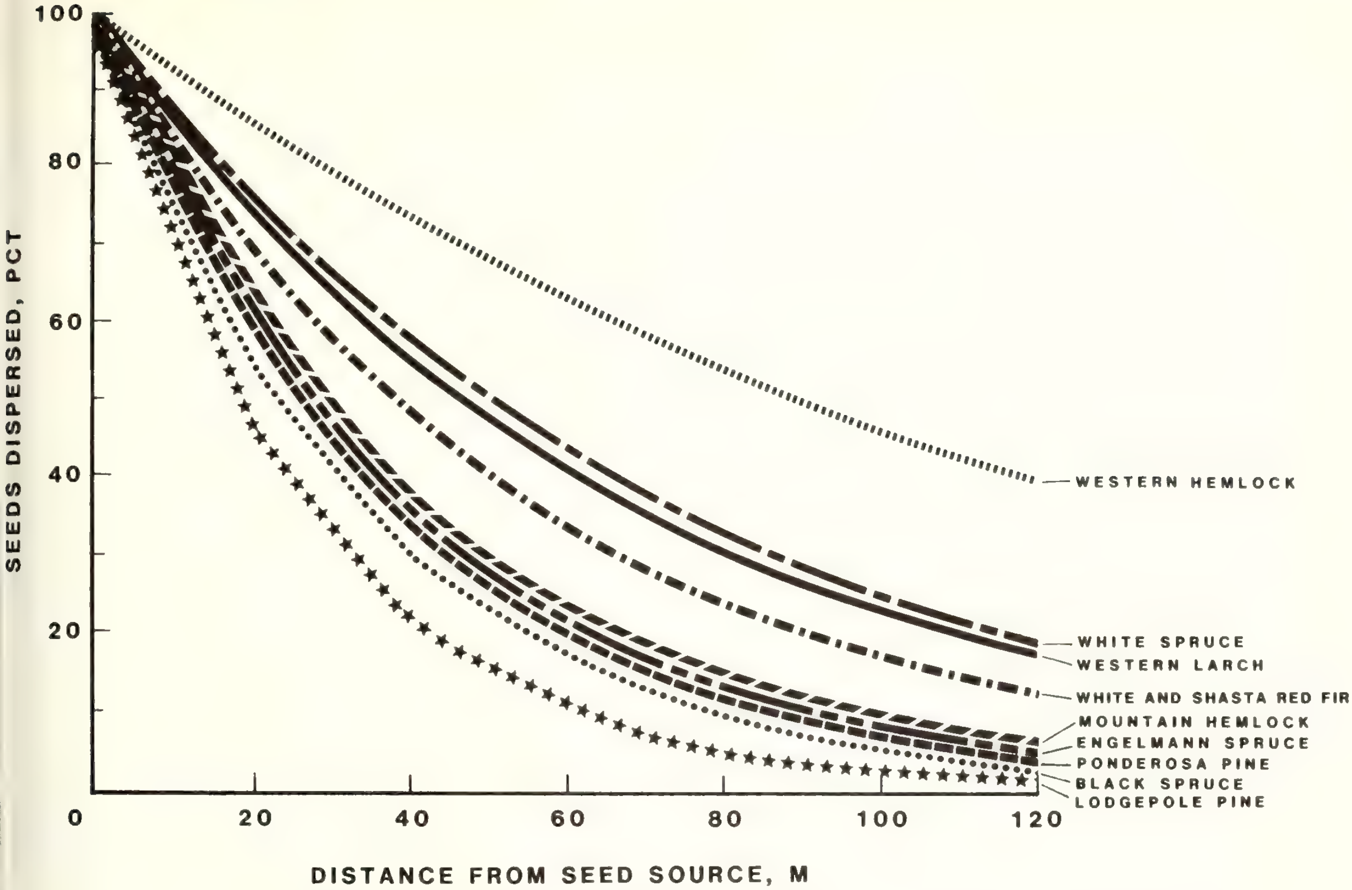

Figure 1.--A comparison of the seed dispersal characteristics of nine conifers of the Inland Mountain West. This relates the number of seeds found at the seed source to the numbers found at increasing distances from the source. Percent values are used to arrive at a common base for the different species.

seeds dispersed to increasing distances. For example, western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) disperses seeds very efficiently but lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) does rather poorly. At 50 m (164 ft), hemlock dispersal was 70 percent while lodgepole pine was only 20 percent of that at the seed source.

It is also apparent that species of the same genus do not necessarily exhibit similar seed dispersal efficiencies. For example, white spruce (*Picea glauca* [Moench] Voss), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and black spruce (*Picea mariana* [Mill.] B.S.P.) range from good to poor in seed dispersal efficiency. The percentage of white spruce seeds reaching 50 m (164 ft) is more than double that of black spruce. Explanations for differences in dispersal efficiencies of these and other species are speculative because definitive data are in short supply.

Mathematical models have been developed for some of the western conifers to illustrate seed dispersal. These models usually fit the data well but offer little explanation of why each species behaves as it does.

Some species, such as Engelmann spruce, have several mathematical models of seed dispersal developed from data collected in different areas within their geographic range (fig. 2). Here, in spite of different independent variables, the dispersal curve shapes are similar. Absolute quantities of dispersed seeds are similar when you consider that one model (Roe 1967) was developed from a bumper crop while the other two models represent several years of seed crop data.

Seed-dispersal patterns of winged-seeded species are influenced by seed and wing length, height and physiographic location of seed source trees, quantity of seed-bearing

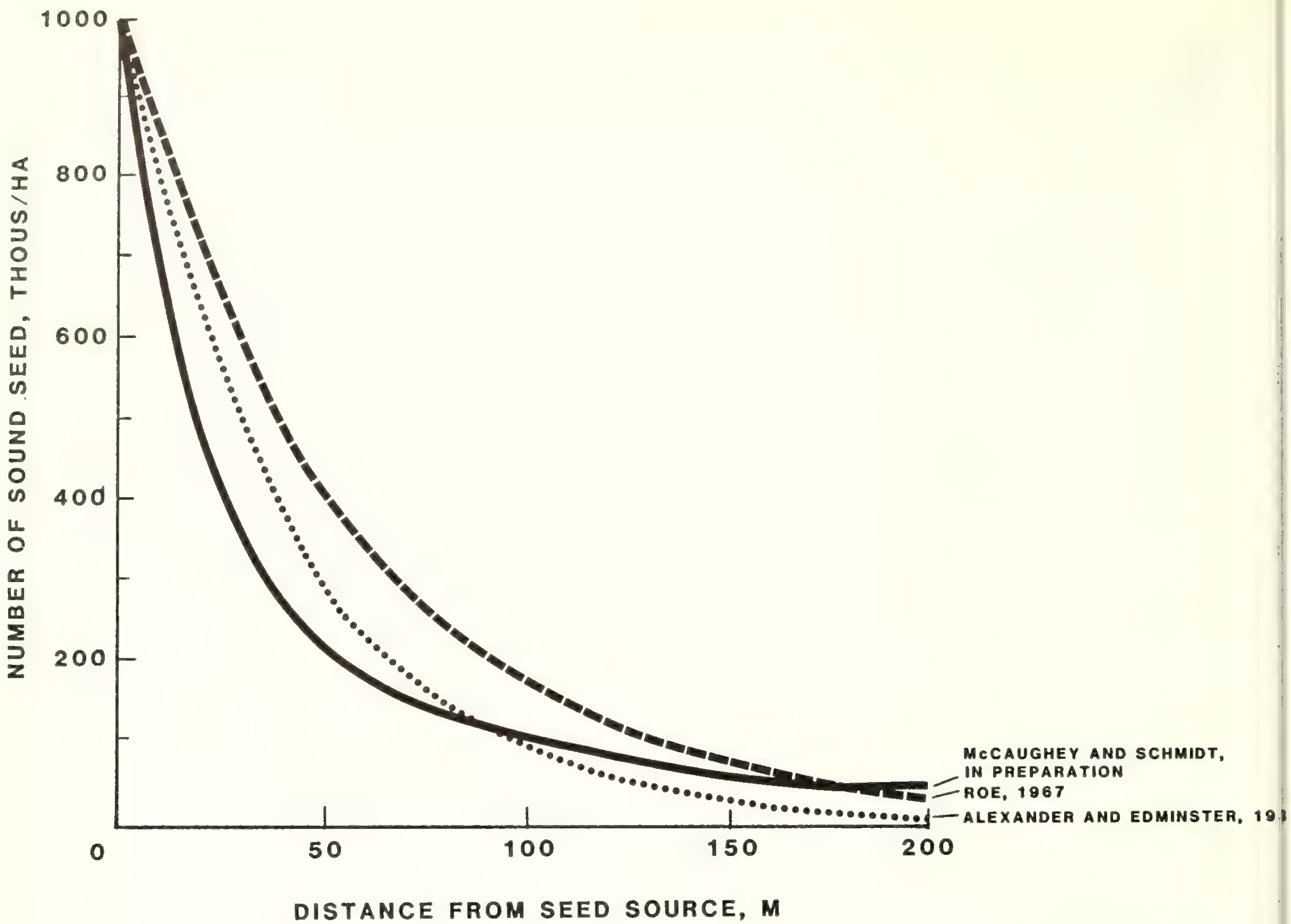

Figure 2.--A comparison of seed dispersal curves from three studies of Engelmann spruce. All three models were calibrated to 1 million seeds per hectare at seed source.

trees, yearly variation of seed production, and time of dispersal. Sharpe and Fields (1982) developed a mathematical model simulating dispersal of winged seeds. Wind speed at the seed source, height of source, and humidity greatly influenced dispersal. Although there are no data to support our claim, small seeds with large wings probably disperse farther than larger seeds with small wings. Seeds likely disperse farther from tall than from short trees and high winds disseminate seeds greater distances than light winds (Isaac 1930). Prevailing winds usually determine the direction of seed dispersal. Rising thermal winds can also disperse seeds uphill in mountainous terrain at mid to lower elevations (Alexander and others 1984; Shearer 1980).

The amount of seed produced is related to the number and character of seed-producing trees. In the Intermountain region the quantity of seed produced was proportional to the square meters of basal area per hectare of Engelmann spruce trees 25.4 cm (10 in) and larger in diameter (Roe 1967; McCaughey and Schmidt in preparation). Each species differs in the frequency of heavy, moderate, and light seed crops. The period between heavy seed crops for various species ranges from about 3 to 10 years. Sound seed production increases linearly with total seedfall, although there is considerable variability between years and locations (Alexander and others 1982).

The following sections present brief descriptions of seed dispersal for each of 23 conifers found within the Inland Mountain West. Table 1 presents descriptions of seed characteristics and cone phenology.

Table 1.--Seed characteristics and tree phenology of some conifers of the Inland Mountain West

Species	Seed characteristics[1]			Phenology[2]	
	Seed length	Wing length	Average number of seeds per kilogram	Cone ripening dates	Primary seed dispersal dates
	mm	mm	Thousands		
Abies					
Grand fir	9.5	19.0	40.6	Aug.	Aug.-Sept.
Subalpine fir	-	-	76.7	Aug.	Sept.-Oct.
White fir	12.7	-	24.5	Sept.-Oct.	Sept.-Oct.
Juniperus					
Rocky Mountain juniper	[3]6.4	none	59.7	Sept.-Dec.	Oct.[4]
Western juniper	-	none	27.1	Sept.	Extended[4]
Larix					
Subalpine larch	-	-	313.1	Aug.-Sept.	Sept.
Tamarack	3.2	6.4	701.1	Aug.-Sept.	Sept.-Spring
Western larch	6.4	12.7	302.0	Aug.	Sept.-Oct.
Picea					
Black spruce	3.2	6.4-9.5	890.1	Sept.	Oct.[5]
Blue spruce	-	-	233.4	Fall	Fall-Winter
Engelmann spruce	3.2	12.7	297.6	Aug.-Sept.	Sept.-Oct.
White spruce	3.2	6.4-9.5	498.2	Aug.	Sept.
Pinus					
Jack pine	2.1	8.5	288.8	Sept.	Sept.[6]
Limber pine	-	-	10.8	Aug.-Sept.	Sept.-Oct.
Lodgepole pine	4.2	12.7	207.2	Aug.-Sept.	Sept.-Oct.[6]
Pinyon	-	-	4.2	Aug.-Sept.	Sept.-Oct.
Ponderosa pine	6.4	25.4	26.5	Aug.-Sept.	Aug.-Sept.
Western white pine	8.5	25.4	59.5	Aug.	Aug.-Sept.
Whitebark pine	-	-	5.7	Aug.-Sept.	Oct.[7]
Pseudotsuga					
Douglas-fir (interior)	-	-	85.5	July-Aug.	Aug.-Sept.
Thuja					
Western redcedar	3.2	3.2	912.7	Aug.-Sept.	Aug.-Sept.
Tsuga					
Mountain hemlock	3.2	12.7	251.5	Aug.-Oct.	Sept.-Oct.
Western hemlock	1.6	-	573.2	Aug.-Oct.	Sept.-Winter

[1]Information from: USDA Forest Service 1974; Harlow and others 1979.

[2]Information from: USDA Forest Service 1965; USDA Forest Service 1974; Schmidt and Lotan 1980.

[3]Cone is 6.4 mm in diameter and has one or two, rarely three or four seeds.

[4]Cones may persist on trees for 2 to 3 years.

[5]Black spruce retains its cones in a semiserotinous state for several years providing a continuous source of seed in stands over 40 years old.

[6]Many serotinous cones remain closed for several months or years.

[7]Seeds are dispersed when the detached cone disintegrates.

Abies

Grand fir.--Wind disperses grand fir (*Abies grandis* [Dougl. ex D. Don] Lindl.) seed in early fall as cones disintegrate and fall from the tree. The seeds are large, and as a result dispersal distances are relatively short. Haig and others (1941) report that fir seed disperses up to 122 m (400 ft) from the source, but 46 to 61 m (150 to 200 ft) was the average dispersal distance. On steep topography of a western Montana site, grand fir seed dispersed upslope nearly 244 m (800 ft) from the nearest source (Shearer 1985).

Grand fir seed dispersal follows the same patterns as the species shown in figure 1. Eight-year results of seed production studies in Idaho showed that grand fir produced the least amount of seed of the species associated with western white pine (USDA Forest Service in press).

Subalpine fir.--Subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) seed is wind-disseminated. Prevailing winds have been found to carry seeds up to 80 m (264 ft) from the windward edge of openings in Colorado (Noble and Ronco 1978). In Montana, Shearer (1980) found that thermal upslope winds dispersed fir seed uphill into clearcuts.

Seed dispersal of subalpine fir follows the typical wind-dispersal pattern (fig. 1). In clearcut openings in Colorado, quantity of seed declined rapidly to about 30 m (100 ft), and then remained at low levels to 80 m (264 ft) from the timber edge (Noble and Ronco 1978). Dispersed seed quantities increase at about 10 m (33 ft) from the leeward edge of the opening, giving a U-shaped distribution profile of dispersal across the openings.

Nobel and Ronco (1978) reported that the velocity of prevailing winds, amount of seed produced, and distance from the source influenced subalpine fir seed dispersal into openings in Colorado. In the mountains of Montana, peak dispersals were usually associated with upslope winds, temperatures greater than average, and humidity levels lower than average (Shearer 1980).

White fir.--White fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.) seed is wind-disseminated as cones disintegrate on the tree in September and October (USDA Forest Service in press). Some seed disperses at least 114 m (375 ft) from the source into openings (Franklin and Smith 1974b). Because fir seed wings are short and broad in relation to seed size, dispersal distances are thought to be small (Gordon 1970; Siggins 1933).

In Oregon, the quantity of white fir seed decreased rapidly from the windward source out to 38 m (125 ft) and then leveled off. Dispersed seed quantities averaged about 25 and 10 percent at 38 m (125 ft) and 114 m (375 ft), respectively, of amounts at the windward source (Franklin and Smith 1974b).

Some white fir seed is dispersed by animals such as the Douglas' squirrel (*Tamiasciurus douglasii* spp.), which cuts and caches fir cones before disintegration (Fowells and Schubert 1956).

Distance was the only measured factor that affected white fir seed dispersal. The quantity dispersed was significantly correlated with distance from the stand edge (Franklin and Smith 1974b). Although only 20 to 50 percent of fir seeds are sound, even in good production years, no significant differences in dispersal distances of sound and empty seeds have been detected (USDA Forest Service 1965; Franklin and Smith 1974b).

Juniperus

Rocky Mountain juniper.--The fruits of Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) are small, indehiscent strobili called "berries" that contain one to four, rarely as many as 12, brownish seeds (USDA Forest Service 1974). The berries are heavy and normally fall close to the parent tree accounting for the slow expansion of juniper forests (Burkhardt and Tisdale 1969). Most of the fruit remains on the tree until late spring. However, after fall ripening, birds and animals have ample time to use it as a food supply. Seed quickly passes through the digestive tracts of birds and animals with little effect on germination capability. Randles (1949) reported that turkeys help disseminate juniper seeds in the Southwest as do bighorn sheep, chipmunks, foxes, and some small mammals. Dispersal of juniper seed depends upon the movement patterns of animals that use the berries as a food source (Randles 1949). The Bohemian waxwing (*Bombycilla garrulus* [Linnaeus]) can eat more than 900 seeds a day and spread them over a wide area (Phillips 1910).

Western juniper.--The fruits of western juniper (*Juniperus occidentalis* Hook.) are small "berries" that contain one to four, rarely as many as 12, brownish seeds. Dispersal occurs when the berries fall off the trees, but usually birds or other animals eat the fruit and disperse the seeds via their excrement (USDA Forest Service 1974). Seedlings are found along fence rows, where they are closely spaced as in a hedge, indicating

that seeds were bird-dispersed. Groups of juniper seedlings are also found beneath other trees to which birds apparently carried juniper seed (USDA Forest Service 1965). Specific information is limited on the types of animals that disperse western juniper seed and how far these animals carry the seed.

Larix

Subalpine larch.--Little is known about seed-dispersal distances of subalpine larch (*Larix lyallii* Parl.). The relatively lightweight, winged seeds fall from the cones in September and are wind-disseminated (USDA Forest Service 1974). Good seed crops occur about once every 10 years. Therefore, seedling establishment is sporadic and limited (USDA Forest Service in press).

Tamarack.--Little information is available on the seed-dispersal characteristics of tamarack (*Larix laricina* [Du Roi] K. Koch). Duncan (1954) reports large numbers of tamarack seedlings located within 1 tree height, a moderate number within 2 tree heights from the seed source, but only scattered seedlings at greater distances. This short dispersal distance is probably explained by the fact that mature seed-producing trees average only 15 to 25 m (50 to 80 ft) tall. Because tamarack seed is winged and wind-dispersed, we assume it follows the same distributional pattern as other wind-dispersed species (fig. 1). Characteristically, tamarack grows in low flat areas, making topographic influences, so common with other western conifers, of lesser consequence. Tamarack seeds are also dispersed by red squirrels (*Tamiasciurus hudsonicus* [Erxleben]), which cut cone-bearing branchlets and cache the cones (Duncan 1954).

Western larch.--Western larch (*Larix occidentalis* Nutt.) seed is small, enabling it to wind-disperse long distances from the source (USDA Forest Service 1965). Numerous studies in Montana have indicated that larch seed disperses at least 250 m (800 ft)(Boe 1953; Shearer 1959; Schmidt and others 1976; Shearer 1985).

The amount of sound larch seed dispersing from the source into clearcuts decreases rapidly out to 122 m (400 ft), and then remains at a low level. Seed crops vary substantially by year, which affects the dispersal pattern. In poor seed years, dispersal beyond 80 m (264 ft) from the timber edge is usually not detected with normal sampling procedures.

Thermal upslope winds in mountain terrain have a direct effect on larch seed dispersal in cuttings on mid to lower elevation slopes in early fall. Cones on upper elevation slopes mature 2 to 4 weeks later than at mid to lower elevations (Fiedler 1976). Therefore, seed is not released during the early fall when thermal upslope winds are prevalent. As a result a high proportion of larch seed on upper slopes is dispersed by storm fronts in mid to late fall (Shearer 1985).

Picea

Black spruce.--The maximum dispersal distance of black spruce (*Picea mariana* [Mill.] B.S.P.) seed is about 100 m (328 ft) from the source (LeBarron 1939; Payandeh and Haavisto 1982). LeBarron (1948) reported that although seed disperses more than 91 m (300 ft) from a source, the number of dispersed seed at 30 m (100 ft) is only 6 percent of the amount of seed falling in the uncut timber.

Dispersal is also affected by windspeed and direction, time of release, and physiographic location, but distance is the only factor that has been quantified. Payandeh and Haavisto (1982) showed that the two variables, stripcut width and distance from the windward stand edge, were highly correlated with the quantity of spruce seed dispersed across a clearcut.

Blue spruce.--We found no specific studies that described seed dispersal of blue spruce (*Picea pungens* Engelm.). Shepperd (1985) speculated that because blue spruce seed is slightly larger than Engelmann spruce, dispersal distances are less. The effective seeding distance, of blue spruce, to obtain adequate natural regeneration, probably is about three to four times the height of the seed-bearing trees.

Engelmann spruce.--Wind, the main disseminator of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) seeds, carries seeds to distances of 244 m (800 ft) from the uncut timber bordering the windward edges of clearcuts (USDA Forest Service in press). In the Intermountain area, wind commonly disseminates spruce seeds to distances of 201 m (660 ft) from the source (Squillace 1954; Roe 1967; McCaughey and Schmidt in preparation). These distances were similar to distances reported for clearcuts in Colorado (Alexander and Edminster 1983). Seeds have also been observed skidding great distances over a glazed snow surface.

General patterns of spruce seed dispersal across clearcuts are shown in figure 2. After an initial rapid decline, the quantity dispersed levels off or gradually declines beyond 100 m (348 ft) from the seed source (Noble and Ronco 1978; Roe 1967). The quantity of dispersed seed increases again at about 10 m (33 ft) from the leeward edge, producing a U-shaped dispersal pattern across openings (Noble and Ronco 1978). Alexander and Edminster (1983) reported that, in Colorado, nearly 40 percent of the spruce seedfall under the uncut windward stand dispersed about 30 m (100 ft), and 10 percent dispersed 91 m (300 ft) from the source. Similar results were found in the Intermountain region where dispersed seed quantities started leveling off at about 120 m (394 ft) from the source (McCaughey and Schmidt in preparation).

Distance from seed source had the greatest impact on the dispersal patterns of Engelmann spruce (fig. 2)(Roe 1967; Noble and Ronco 1978; Alexander and Edminster 1983; McCaughey and Schmidt in preparation). Also, studies in the Intermountain area show that quantity of seeds dispersing into clearcuts is strongly correlated with basal area of mature spruce in the adjacent uncut timber. As stand basal area of mature spruce 25 cm (10 in) and larger increased, quantity of dispersed seed increased (Roe 1967; McCaughey and Schmidt in preparation). Colorado studies also show a strong positive correlation of seedfall under the uncut stand with quantity dispersed into clearcuts (Alexander and Edminster 1983; Noble and Ronco 1978).

White spruce.--White spruce (*Picea glauca* [Moench] Voss) has very small seeds, which wind disperse in the air and over snow. Early studies indicated 101 m (330 ft) was the greatest distance seeds disseminated via air, but with sufficient wind much greater distances would be expected (Rowe 1955). Late-falling seeds were blown considerable distances over crusted snow (Rowe 1955). Nearly 88 percent of seeds fall in September, the first month of dispersal, with the remaining seeds dispersing during the winter and spring (Crossley 1955). About 20 percent of the total seeds dispersing during the winter were trapped beyond 100 m (328 ft), and 9 percent beyond 200 m (656 ft) from the source. The presence of seedlings indicated that spruce seed dispersed at least 300 m (984 ft) from the stand edge in strip and clearcuttings (Dobbs 1976).

Quantity of dispersed spruce seed decreases rapidly from timber edge to about 140 m (460 ft) into clearcuts, and then levels off for a considerable distance from the source. This pattern suggests that significant quantities of seed are released in high winds (Dobbs 1976).

Pinus

Jack pine.--Jack pine (*Pinus banksiana* Lamb.) has two seed dispersal modes because its cones are serotinous and nonserotinous. Although seeds are winged and small, about 2.1 mm (0.33 in) long, they have a relatively short dispersal distance. We found no studies that described seed dispersal from nonserotinous cones. However, indirect evidence of dispersal through seedling establishment suggests the effective dispersal range is about 34 to 40 m (110 to 130 ft)--2 tree heights--but, the number of established seedlings more than 1 tree height from the seed source is low (USDA Forest Service 1939). Seed dispersal distances from serotinous cones are very short because cones must be near the ground surface before ambient air temperatures are high enough to melt the resin bond. Cameron (1953) reported that the bonding resin on serotinous cones melts at about 50 °C (122 °F).

Limber pine.--Limber pine (*Pinus flexilis* James) seeds are very large and have rudimentary wings or are wingless (Harlow and others 1979). Because of their large size, they are seldom dispersed by wind. The primary disperser in northern Utah, Wyoming, and Arizona (and presumably throughout the range of limber pine) is the Clark's nutcracker (*Nucifraga columbiana* [Wilson])(Tomback and Kramer 1980; Benkman and others 1984). Nutcrackers carry seeds to caches under forest litter. Some of these cache sites are favorable to germination (Tomback 1981). Red squirrels cache cones under deep litter piles where seeds are unlikely to germinate (Benkman and others 1984). Presumably, birds can disperse these seeds great distances, but animal, wind, and gravity dispersal likely provide limited distribution.

Lodgepole pine.--Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) has the smallest seeds of any pine except jack pine. Yet, dispersal distances are far less than such associates as western larch and Engelmann spruce. Seeds from nonserotinous cones, sufficient to restock cutover areas, seldom disperse over 61 m (200 ft) from the source (Boe 1956; Perry and Lotan 1977a). However, in western Montana winds dispersed seeds uphill nearly 244 m (800 ft) from the downhill side of clearcuts (Shearer 1985). Seeds have been observed skidding great distances over a glazed snow surface.

Dispersal distances for seeds from serotinous cones depend upon the distance cones are scattered during logging. Serotinous cones need temperatures near 60 °C (140 °F) to break resin bonds. Fire will easily melt the resin bond, but cones must be within 30 cm (12 in)

of the ground before ambient air temperatures are high enough to open the cones (Perry and Lotan 1977b; Lotan and Perry 1983). Eighty-three percent of serotinous cones on south slopes and 40 percent on north slopes open when they are less than 30 cm (12 in) above the ground (Lotan 1964).

Quantity of lodgepole seed decreases rapidly as distance from the source increases--at 20 m (66 ft) into clearcuts seedfall varies from about 10 to 30 percent of that at timber edge (Boe 1956; Dahms and Barrett 1975; Lotan and Perry 1983). At 20 m (66 m) from the windward side (fig. 1) the seedfall is about 45 percent of that at stand edge. A U-shaped distribution occurs between stand edges across clearcuts (Lotan and Perry 1983).

Wind disperses lodgepole seeds from nonserotinous cones, but seed from serotinous cones is usually dispersed by scattering conebearing slash throughout logging areas. Seed dispersal distances are likely to be greater on south than on north slopes because of higher velocities of thermal upslope winds on warmer south-facing slopes (Fiedler 1974).

Pinyon.--Seed dispersal characteristics are similar for pinyon (*Pinus edulis* Engelm.) and singleleaf pinyon (*Pinus monophylla* Torr. and Frem.), therefore, they are presented together.

The large seeds of pinyon are dispersed by gravity or animals since the seed wing is easily detached, and of no practical use in dispersal (Phillips 1909). Clark's nutcrackers cache seeds long distances from the source, 1 to 3 cm (.4 to 1.2 in) below the soil surface in open areas (Vander Wall and Balda 1977; Lanner and Vander Wall 1980). Some cached seeds, not utilized by nutcrackers during the winter months, germinate and thus expand pinyon distribution. Everett (1985) speculates that rodents disperse seed locally under, or short distances from, existing pinyon stands. Preliminary results indicate that nearly 87 percent of seedlings are located under or near fully stocked stands. Rasmussen (1941) reported that woodrats (*Neotoma* spp.), mice (*Peromyscus* spp.), and chipmunks (*Eutamias minimus* spp.) cached pinyon seeds, but whether caches were on sites favorable for germination was unknown.

Ponderosa pine.--Seed dispersal information presented here is for ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), since little information is available for Arizona pine (*Pinus ponderosa* var. *arizonica* [Engelm.] Shaw) and Rocky Mountain ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.).

Ponderosa pine seeds are fairly large, and as a result do not disseminate great distances (Barrett 1966). Theoretical calculations of seed flight indicated that a 30-m (100-ft) tree exposed to 32-km/h (20-mi/h) winds would disperse seeds up to about 180 m (594 ft) (Siggins 1933). Data indicate that most seeds fall within 20 to 40 m (60 to 132 ft) from seed-producing trees (Curtis and Foiles 1961; Barrett 1966). However, a minor amount of seed will disperse up to 160 m (528 ft) in central Oregon and 244 m (800 ft) in western Montana (Barrett 1966; Shearer 1985). In Idaho, 82 percent of the seed dispersed within 152 m (500 ft) of the timber edge was confined to 30 m (100 ft) of the edge. Some of the seed falls to the ground in cones (USDA Forest Service 1940). Seed is released when high ground temperatures dry out the cones causing scales to open (Curtis and Foiles 1961).

Western white pine.--Western white pine (*Pinus monticola* Dougl. ex D. Don) seed is mainly wind dispersed, although squirrels, mice, and birds disseminate some seed. Clumps of seedlings have been found where seeds cached by mice have germinated (USDA Forest Service 1965). Seeds are large and do not disperse great distances. Haig and others (1941) reported that seed sufficient for adequate reproduction seldom reaches more than 122 m (400 ft) from the source. Isaac (1930) demonstrated that when white pine seed was dropped from a height of 61 m (200 ft), in a 21 km/h (13 mi/h) wind, it dispersed 792 m (2,600 ft) from the point of release. Shearer (1985) reported that white pine seeds dispersed at least 244 m (800 ft) uphill from the source at the bottom edge of steep mountain clearcuts in Montana.

Whitebark pine.--Little information is available on the seed-dispersal characteristics of whitebark pine (*Pinus albicaulis* Engelm.). Its large seeds are wingless and disseminate after the cones detach from the tree and disintegrate (USDA Forest Service 1974). The primary disseminators are animals, especially the Clark's nutcracker. A single nutcracker eats up to 32,000 seeds per year. These birds store whitebark seeds in small caches on the ground, some on microsites favorable for germination. This dispersal by nutcrackers helps maintain the "pioneering" status of whitebark pine (Tomback 1981).

Squirrels also collect and cache whitebark pine cones and seeds, often carrying them great distances from the source. Bears also feed on the seeds, especially grizzly bears (*Ursus arctos* [Linnaeus]), which depend heavily on these seeds as an important source of energy, particularly in the Yellowstone

ecosystem. Some seeds pass through the bear's digestive system intact; therefore, bears may serve as a minor mode of dispersal.

Pseudotsuga

Rocky Mountain Douglas-fir.--Rocky Mountain (interior) Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) has moderate-size seeds and seed wings and is wind-disseminated. Boe (1953) reports that large quantities of seeds dispersed up to 80 m (264 ft) from the source in clearcuts on the Coram Experimental Forest in northwestern Montana. Seed also disperses into clearcuts on steep topography up to 244 m (800 ft) uphill from the source (Shearer 1985). Reproduction indicates a seed-dispersal radius of about 91 to 183 m (300 to 600 ft) around open-grown trees on level land (Frothingham 1909).

Douglas-fir has a seed-dispersal pattern similar to other species (fig. 1). Quantity of dispersed seed decreases rapidly out to 80 m (264 ft) and remains at low levels from 80 to 241 m (264 to 792 ft) from the source (Boe 1953). Shearer (1985) reported that early-ripening seeds were dispersed by upslope thermal winds and late-ripening seeds by winds of unstable air masses from storm fronts.

Thuja

Western redcedar.--Western redcedar (*Thuja plicata* Donn ex D. Don) seed is wind-disseminated, but because of a small wing surface, its rate of fall is fast and flight distance is short (Siggins 1933). Isaac (1930) reports that seed did not disperse more than 122 m (400 ft) when released at 46 m (150 ft) above the ground. However, in British Columbia, an examination of regeneration indicated that seed dispersed at least 201 m (660 ft) from the source (Clark 1970).

The pattern of redcedar seed dispersal is apparently similar to patterns shown for other conifer species (fig. 1). Nearly 80 percent of filled seeds in clearcuts are found within 15 to 30 m (50 to 100 ft) from the source. (Gashwiler 1969). Seeds, dispersed between 61 to 76 m (200 to 250 ft) from the source, accounted for 17 percent of the total seed count in clearcuts with only 4 percent dispersing 107 to 122 m (350 to 400 ft).

Tsuga

Mountain hemlock.--Seeds of mountain hemlock (*Tsuga mertensiana* [Bong.] Carr.) are small, and have a large wing, making them well-suited for wind dispersal. Mountain hemlock is a prolific seed producer and bears seed nearly every year (USDA Forest Service 1965). Its seed disperses at least 114 m (375 ft) into clearcuts from the source (Franklin and Smith 1974a).

The dispersal pattern of mountain hemlock is very similar to Engelmann spruce (fig. 1). Quantity of hemlock seed decreases rapidly from the source out to about 38 m (125 ft), and then levels off at a low level or decreases slowly from 38 to 114 m (125 to 375 ft) (Franklin and Smith 1974a). The amount of seed dispersed at 120 m (394 ft) from the source is less than 10 percent of that at the source (fig. 1).

Mature seed-producing trees are relatively short, usually 15 to 23 m (50 to 75 ft). Were it not for this, seed-dispersal distances would likely be much greater. The number of seed-bearing trees in adjacent stands also influences the amounts of seed dispersed into clearcuts (Franklin and Smith 1974a).

Western hemlock.--Western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) seeds are light and are dispersed great distances by wind. During bumper crop years, enough seed falls within 100 m (330 ft) from the source to provide optimum seedling establishment (Clark 1970). To produce sufficient seed for adequate stocking 201 m (660 ft) from the source, at least two bumper seed crops are usually required.

Considerable amounts of hemlock seed have been observed dispersing up to 610 m (2,000 ft) from the source. In a controlled test, hemlock seeds released at a height of 61 m (200 ft) in a 20.1 km/h (12.5 mi/h) wind dispersed as far as 1 158 m (3,800 ft)(Isaac 1930). In our comparisons of dispersal curves (fig. 1), western hemlock stood out as the most efficient of the western conifers. For example, the number of seeds dispersed to 120 m (394 ft) was nearly half of the number dispersed to the stand edge. This was about double that of any other associated species.

Hemlock seed disseminates from cones throughout fall and early winter months. During the winter, winds sometimes disperse seeds across crusted snow, depositing large amounts in small depressions (Harris 1969).

DISCUSSION

Managers depending on natural regeneration in their silvicultural practices should consider seed dispersal characteristics in their plans. This paper synthesizes information available for our western conifers. Of this information the following factors stand out as being very important in describing seed dispersal:

1. Wind is the primary dispersing mechanism for seeds of western conifers.

2. The shapes of seed dispersal curves are very similar for most western conifers, but species vary substantially in dispersal distances.

3. Of the tree, stand, and site characteristics that largely determine the dispersal patterns of western conifers, several stand out:
   - seed aerodynamics
   - tree height
   - time of dispersal
   - character of the seed-producing stand (size and number of each species)
   - annual variability of seed production
   - physiographic position of seed source as related to wind character.

4. Thermal winds are very important for early season dispersal of seeds; prevailing winds and storm fronts are very important for late season dispersal.

5. Most seeds are dispersed through the air in the fall, but seeds released in late fall and early winter may also be blown over crusted snow.

6. Birds and mammals are the primary dispersal agents for wingless seeds and can carry them for substantial distances.

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CONE PRODUCTION ON DOUGLAS-FIR AND WESTERN LARCH IN MONTANA

Raymond C. Shearer

ABSTRACT: This study determined the number of cones that matured on Douglas-fir and western larch growing on twenty 0.1-ha (0.25-acre) plots from 1980 through 1983 at each of four locations near Missoula, MT. A good cone crop in 1980 produced 80 percent of all cones counted during the 4-year study. In 1980, cones were produced on 45 percent of the Douglas-fir and 38 percent of the larch in the 10- to 15-cm (4- to 6-inch) diameter class while 85 percent were produced by both species in the 30- to 36-cm (12- to 14-inch) diameter class. The average number of cones per tree in 1980 increased 10 times for Douglas-fir and 27 times for larch as the diameter classes increased from 10 to 15 cm (4 to 6 inches) to 30 to 36 cm (12 to 14 inches). In years of fair or poor cone production the average number of cones per tree was about seven times greater for Douglas-fir and 15 times greater for western larch in the 30- to 36-cm (12- to 14-inch) diameter class than in the 10- to 15-cm (4- to 6-inch) diameter class. More than half of the Douglas-fir and larch in the 10- to 15-cm (4- to 6-inch) diameter class failed to produce any cones during the study; only 7 percent of the trees in the 30- to 36-cm (12- to 14-inch) diameter class failed to produce cones.

INTRODUCTION

Cone production in natural forest stands has been studied at several locations in the Inland Mountain West (Fowells and Schubert 1956; Franklin and others 1974; Alexander and Noble 1976). Cone production of conifers native to Montana was studied by Boe (1954). He classified Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) west of the Continental Divide as a prolific seeder and western larch (*Larix occidentalis* Nutt.) as a good seeder.

Cone production either on individual trees or within natural stands usually varies greatly by year. Because Douglas-fir and larch cones develop throughout the crowns, trees of greater diameter and crown volume usually produce more cones (Fowells 1965). The purpose of this study was to determine for Douglas-fir and larch at four study sites in western Montana from 1980 through 1983: (1) the influence of insect larvae, particularly western spruce budworm (*Choristoneura occidentalis* Freeman), on cone and seed losses (Hedlin and others 1980) and (2) the number of cones produced each year. Shearer (1984) published information on the cone and seed reduction caused by insect feeding. This paper reports the number of cones that were produced on the Douglas-fir and larch growing within each of 80 plots.

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STUDY SITES

In 1980, four study sites were selected near Missoula in western Montana. Two were in the warm and dry Douglas-fir forest series and two in the cooler and moister subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) forest series (Pfister and others 1977):

Forest series	Distance and direction of sites from Missoula, MT
Douglas-fir	Ashby Creek (Ashby) 29 km (18 miles) east
	Blue Mountain Road (Blue) 8 km (5 miles) southwest
Subalpine fir	West Fork Lolo Creek (Lolo) 35 km (22 miles) southwest
	Spring Creek (Spring) 60 km (36 miles) northeast

The study sites are identified hereafter by the names in parentheses.

Ashby is a second-growth stand averaging 50 years old, composed of 35 percent Douglas-fir, 24 percent western larch, 20 percent Rocky Mountain ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.), and 21 percent lodgepole pine (*P. contorta* var. *latifolia* Engelm.). Blue, a partially cut stand averaging 80 years old, is composed of 67 percent Douglas-fir, 29 percent western larch, and 4 percent ponderosa pine. Lolo, a partially cut stand averaging 70 years of age, is composed of 15 percent Douglas-fir, 35 percent western larch, 48 percent lodgepole pine, and 2 percent ponderosa pine, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and subalpine fir. Spring is a more open partially cut stand with trees ranging from 60 to 175 years of age. Composition of the

cone-bearing trees is 30 percent Douglas-fir, 42 percent western larch, 13 percent subalpine fir, 8 percent lodgepole pine, 6 percent Engelmann spruce, and 1 percent ponderosa pine.

At each of these four study sites, twenty 0.1-ha (0.25-acre) circular plots were randomly established. All trees 8 cm (3 inches) d.b.h. and larger were numbered. Trees were grouped into 5-cm (2-inch) diameter classes for this paper: 10 cm [10.2-15.0] (4-inch) [4.0-5.9], 15 cm [15.2-20.1] (6-inch) [6.0-7.9], for example. Broader groupings were also used; for example, 10-15 cm (10.2-20.1 cm) [4-6 inch (4.0-7.9 inch)] and 20-25 cm (20.2-30.2 cm) [8-10 inch (8.0-11.9 inch)].

The number of trees per acre was greatest at Blue, followed by Lolo, Ashby, and Spring (table 1). Each location had both Douglas-fir and larch in the 10- through 36-cm (4- through 14-inch) diameter classes. Douglas-fir and western larch were most abundant in the 15-cm (6-inch) diameter class at each location. Only occasional larger diameter trees grew within the plots.

Table 1.--Average number of Douglas-fir (PSME), western larch (LAOC), and other trees per acre by diameter class, forest series, and study area in western Montana, 1980. Basis: twenty 0.1-ha (0.25-acre) plots at each location

Diameter class	PSME	LAOC	Other	PSME	LAOC	Other
	Pseudotsuga menziesii Forest Series					
	Ashby Creek			Blue Mountain		
4	7.4	3.8	0.8	7.6	6.4	
6	19.8	13.2	18.6	50.8	20.4	3.0
8	10.6	8.4	14.0	40.6	16.2	1.8
10	6.2	5.0	10.2	23.4	9.2	1.4
12	3.6	2.2	7.4	6.6	4.2	.6
14	.8	1.0	4.0	1.2	.6	.2
16	.4		1.4	.2	.2	.4
18	.2		1.0			
20			.4			.2
Sum	49.0	33.6	57.8	130.4	57.2	7.6
	Abies lasiocarpa Forest Series					
	Lolo Creek			Spring Creek		
4	1.0	1.0	1.4	7.2	3.2	6.6
6	11.4	28.0	35.2	7.6	15.4	7.8
8	5.0	17.6	27.4	3.8	9.8	3.6
10	3.4	6.4	13.8	3.6	1.6	3.6
12	2.6	3.4	4.8	.6	3.2	.6
14	.4	1.0	.2	.6	.4	.2
16	.2	.6				
18	.2			.6		
22		.4				
30		.4				
Sum	24.2	58.8	82.8	24.0	33.6	22.4

The Blue study area had 1.1 to 2.8 times more total basal area than the other three locations; Spring had only 0.4 as much as the other sites (table 2). Blue had from 2.7 to 6.0 times more Douglas-fir basal area and from 0.9 to 1.8 times more larch than the other stands.

Table 2.--Basal area (ft^2/acre) of Douglas-fir (PSME), western larch (LAOC), and other trees by forest series and study area in western Montana, 1980. Basis: twenty 0.1-ha (0.25-acre) plots at each location

Forest series	Plot	PSME	LAOC	Other	Total
Douglas-fir	Ashby	20.1	13.9	34.1	6[illegible].1
	Blue	54.7	24.2	4.4	8[illegible].2
Subalpine fir	Lolo	11.0	27.8	34.5	7[illegible].3
	Spring	9.1	13.1	7.5	2[illegible].7

CONE PRODUCTION ESTIMATES

Douglas-fir and western larch cone production was estimated in 1980, 1981, 1982, and 1983 on the 80 plots by counting the fully elongated cones between late July and early September. No attempt was made to judge the amount of cone mortality from bud burst to the time of examination. Cone counts on trees of other coniferous species growing on the plots were not made.

In 1980, counts were made from a truck-mounted hydraulic bucket. In 1981, 1982, and 1983, cones were counted on each tree from points where the full length of the tree could be scanned with binoculars. Trees that produced no or few cones (usually less than 10 cones), were carefully examined to be sure no cones were missed. This meant observing these trees from two or more locations so the entire crown could be scanned. Trees with greater numbers of cones were examined from only one location.

RESULTS

The average total number of mature cones per tree counted from 1980 through 1983 varied by species and by study location (table 3). Douglas-fir averaged greater total 4-year cone production than western larch at Ashby, Lolo, and Spring. These numbers were substantially lower than the potential because of insect-caused mortality in the early development of the conelets (Shearer 1984). Cone production of both species was greatly influenced by year and diameter class.

Table 3.--Average number of Douglas-fir and western larch cones per tree and number of trees sampled per year by study area, western Montana

Year	Study area	Douglas-fir: Average and standard deviation	Douglas-fir: Trees	Western larch: Average and standard deviation	Western larch: Trees
		Number		Number	
1980	Ashby	219 ± 318	206	147 ± 274	134
	Blue	46 ± 141	497	107 ± 238	192
	Lolo	187 ± 300	61	74 ± 271	132
	Spring	287 ± 428	58	159 ± 340	113
1981	Ashby	<1 ± <1	241	7 ± 16	167
	Blue	0 ± 0	600	1 ± 2	275
	Lolo	<1 ± 3	120	3 ± 12	291
	Spring	<1 ± <1	107	3 ± 12	163
1982	Ashby	8 ± 23	240	9 ± 19	167
	Blue	64 ± 99	590	31 ± 52	271
	Lolo	101 ± 82	82	19 ± 51	265
	Spring	20 ± 119	119	3 ± 11	168
1983	Ashby	<1 ± 1	144	21 ± 47	115
	Blue	<1 ± <1	621	10 ± 29	283
	Lolo	<1 ± <1	64	3 ± 10	206
	Spring	9 ± 25	119	10 ± 35	167

Production by Year

About 80 percent of all Douglas-fir and western larch cones counted during the 4 years of this study were produced in 1980. Twenty percent of the Douglas-fir cones were counted in 1982, and less than 1 percent in 1981 and 1983. Two, 11, and 7 percent of the larch cones were counted in 1981, 1982, and 1983.

The average number of cones per tree also varied each year by location (table 3). Greatest average cone maturity for the 4-year period occurred at Spring, where average basal area and crown competition were least. Lowest cone production occurred at Blue, where the highest basal area was measured. Although most of the Douglas-fir cones were produced in 1980, more cones matured at Blue in 1982 than in 1980 (table 3). This difference would have been even greater if insect-caused mortality of conelets in 1982 was kept at the same level as in 1980 (Shearer 1984). The low Douglas-fir cone counts in 1983 at Ashby and Blue resulted from high conelet mortality caused by insects.

Production by Diameter Class

More Douglas-fir and larch cones were produced on larger diameter trees, probably because of greater crown volume. In 1980, cone production at least tripled in each larger diameter class (table 4). This trend was similar at all locations, although the average number of cones varied from lower counts at Blue to higher counts at Spring. The number of Douglas-fir cones on each tree ranged from 0 to 698 in the 10- to 15-cm (4- to 6-inch) (small) diameter class, 44 to 1,065 in the 20- to 25-cm (8- to 10-inch) (mid) diameter class, and 81 to 1,482 in the 30- to 36-cm (12- to 14-inch) (large) diameter class. The number of western larch cones on each tree ranged from 0 to 750 within the small diameter class, 0 to 1,200 within the mid diameter class, and 0 to 2,450 within the large diameter class.

Cone production in 1981, 1982, and 1983 was much lower than in 1980. Nevertheless, the average number of Douglas-fir and western larch cones per tree increased in each larger diameter class except in 1981 when so few Douglas-fir cones were produced that the trend was not evident (table 4). One Douglas-fir at Lolo had 30 cones--the greatest number found in the four study areas. Most western larch also failed to produce cones in 1981 and the maximum number of cones was 85, 130, and 55 in the small, mid, and large diameter classes.

The number of Douglas-fir cones in 1982 ranged from 0 to 360 within the small, 0 to 550 within the mid, and 0 to 400 within the large diameter classes; larch cones ranged from 0 to 150 within the small, 0 to 250 within the mid, and 0 to 300 within the large diameter classes.

In 1983, cone production on Douglas-fir ranged from 0 to 66 within the small, 0 to 104 within the mid, and 0 to 176 within the large diameter classes. Larch cone production in 1983 ranged from 0 to 57 within the small, 0 to 117 within

Table 4.--Average number of Douglas-fir and western larch cones per tree and number of trees sampled each year by diameter class for four locations, western Montana

Year	Diameter class	Douglas-fir: Average and standard deviation	Douglas-fir: Trees	Western larch: Average and standard deviation	Western larch: Trees
	Inch	Number		Number	
1980	4- 6	41 ± 114	377	21 ± 79	261
	8-10	132 ± 232	366	116 ± 210	247
	12-14	434 ± 519	63	575 ± 536	55
1981	4- 6	<1 ± 1	509	1 ± 5	444
	8-10	<1 ± <1	464	4 ± 13	361
	12-14	0 ± 0	77	6 ± 12	78
1982	4- 6	17 ± 49	490	5 ± 16	434
	8-10	72 ± 99	450	26 ± 47	348
	12-14	122 ± 139	72	48 ± 78	76
1983	4- 6	<1 ± 4	434	1 ± 5	376
	8-10	1 ± 7	426	9 ± 17	319
	12-14	6 ± 26	70	56 ± 82	69

the mid, and 0 to 272 within the large diameter classes.

The percentage of trees that produced cones increased with size of cone crop:

Size of cone crop	Douglas-fir	Western larch
1 (largest)	49 (1980)	48 (1980)
2	43 (1982)	24 (1983)
3	2 (1983)	22 (1982)
4 (smallest)	<1 (1981)	13 (1981)

In 1981, of 1,050 Douglas-fir trees examined, only seven produced cones. In 1983, 2, <1, and 3 percent of the trees at Ashby, Blue, and Lolo produced cones. At Spring, however, 24 percent of the trees produced cones. The 1982 and 1983 larch cone crops had about half as many trees produce cones as in 1980. As more trees produced cones, the average number of cones per tree also increased.

The percentage of trees that had cones increased in the larger diameter classes. An average of only 13 percent of the larch in 1981 produced cones; in the small, mid, and large diameter classes, 5, 18, and 32 percent of the trees yielded cones (table 5). Cones were on 49 percent of the Douglas-fir and 48 percent of the larch in 1980. In Douglas-fir, 45, 60, and 86 percent of the small, mid, and large diameter classes produced cones (table 5). In western larch 38, 50, and 84 percent of the small, mid, and large diameter classes had cones. The Douglas-fir cone crop of 1982 matured cones on 22, 60, and 75 percent in the small, mid, and large diameter classes. The larch cone crops o 1982 and 1983 produced cones on an average of 12, 27, and 58 percent in the small, mid, and large diameter classes.

Table 5.--Percent of Douglas-fir and western larch in four western Montana study areas that had 0, 1-99, and more than 99 cones per tree each year by diameter class

Year	Diameter class	Douglas-fir 0	Douglas-fir 1-99	Douglas-fir >99	Western lar 0	Western lar 1-99	Western lar >
1980	4- 6	55	33	12	62	35	
	8-10	40	29	31	50	32	
	12-14	14	22	64	16	14	
1981	4- 6	100	0	0	95	5	
	8-10	>99	<1	0	81	18	
	12-14	100	0	0	68	32	
1982	4- 6	78	16	6	84	15	
	8-10	40	29	31	78	14	
	12-14	25	35	40	48	29	
1983	4- 6	98	2	0	91	9	
	8-10	98	2	0	68	30	
	12-14	95	2	3	36	42	

The frequency of cone production varies by species (table 6). During these 4 years, larch had cones more frequently than Douglas-fir. Although 34 percent of the trees of both specie failed to have any cones, 26 percent of the larch and only 1 percent of the Douglas-fir had

cones in 3 or in all 4 years. The remaining 40 percent of the larch and 65 percent of the Douglas-fir produced cones 1 or 2 of the 4 years.

Table 6.--Percent of Douglas-fir and western larch trees in four western Montana study areas that had one or more cones during the 4 years of the study by species and diameter class

Species	Diameter class	Number of years cones produced				
		0	1	2	3	4
Douglas-fir	4- 6	51	38	11	0	0
	8-10	24	35	40	1	0
	12-14	7	25	65	3	0
Western larch	4- 6	54	27	11	7	1
	8-10	22	17	24	27	10
	12-14	6	4	36	33	21

As the diameter increased, the frequency of cone production usually increased (table 6). For example, 11, 41, and 68 percent of the Douglas-fir and 19, 61, and 90 percent of the larch of the small, mid, and large diameter classes had cones 2, 3, or 4 years of the study. More than half of the Douglas-fir and larch trees in the small diameter class failed to produce cones any of the 4 years; less than one-fourth and one-tenth of the mid and large diameter classes failed to produce cones in any of the 4 years.

MANAGEMENT IMPLICATIONS

Although Douglas-fir produced more cones per tree than did western larch during the 4 years of this study, larch produced some cones every year; Douglas-fir nearly failed to produce cones in 2 of the years. Where seed production is an important consideration, larger diameter full-crown dominant and codominant Douglas-fir and western larch should be reserved because larger trees produce more cones more frequently than smaller diameter trees. The number of mature Douglas-fir cones tripled from the small to the mid diameter class and tripled again from the mid to the large diameter class. Western larch cones increased fivefold through each of the diameter class comparisons.

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CONE PRODUCTION IN *PINUS ALBICAULIS* FORESTS

T. Weaver and F. Forcella

ABSTRACT: Whitebark pine cone production was estimated for a 6 to 8 year period in each of 29 stands widespread in the northern Rocky Mountains. 1) One-time sampling was possible since the estimate was made by multiplying the number of branches per m^2 by an estimate of annual cone production made from counts of conelets, mature cones, or cone scars on successively older annual increments of those branches. 2) Average cone production ranged from 0.3 to 3.6 cones$\cdot m^{-2} \cdot yr^{-1}$ and from 22-270 seeds$\cdot m^{-2} \cdot year^{-1}$. 3) Regression analysis was used to relate the variance observed to time and place. a) Year-to-year variation in the cone yield of branches, trees, and stands in a region appears to be both internally and externally controlled. Internal control is suggested by the fact that good cone years were usually preceded by poor cone years. While external control is indicated by significant correlations between growth and weather conditions, control is not dominated by the effect of any one factor or any particular developmental stage. b) Although cone production of the average branch varied significantly within 30 percent of the trees and within 48 percent of the stands observed, it did not vary significantly among stands. c) Regressions relating stand cone production to easily measured stand characteristics such as canopy cover, fallen cones, and/or stand size explain no more than 50 percent of the variance among stands.

INTRODUCTION

Pinus albicaulis (whitebark pine) is a dominant or codominant tree in many high-altitude forests of western North America (Weaver and Dale 1974; Arno 1986). Its large, well-provisioned seeds are important not only for their reproductive function, but also as food for man, bears, squirrels, and nutcrackers (Blankenship 1905; Forcella and Weaver 1980; Kendall 1980b; Hutchins and Lanner 1982; Tombach 1983). Managers considering either of these functions might ask: What is average production? How does it vary between stands? How does it vary between years? And how might I estimate these variables in an unstudied stand?

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This paper (1) demonstrates a method for estimating a stand's cone production over a 6 to 8 year period after a single sampling, (2) reports estimates made in 29 stands widespread in the northern Rocky Mountains, and (3) uses that data set both to determine the relationship of yield to easily measured stand characteristics and to determine the relationship of yield to regional weather conditions.

METHODS

Cone production.--Cone production in the 1969 through 1976 period was estimated for 29 *P. albicaulis* stands from the Montana-Idaho border [Bitterroot (5 stands) and Salmon River (2) Mountains], from southwest Montana [Little Belt (1), Big Belt (3), Castle (3), Elkhorn (2), Pioneer (1), Tobacco Root (2), Madison (3), and Bridger Mountains (1)] and from western Wyoming [Absaroka (3), and Wind River Mountains (3)]. More exact locations are given by Forcella (1977).

The measurements necessary for these estimates were made as follows:

1. Current, future, and past production were determined for 25 representative shoots, that is five shoots each from the tops of five representative trees.

2. The number of shoots per m^2 in the canopy was determined by counting the potential cone bearing leaders on each of the five trees and dividing by a canopy area calculated from the tree's greatest and least canopy diameters.

3. Tree cover in the study area was determined as a percent of 90 overhead points covered by the canopy; the points were examined through a vertical periscope held at meter intervals along three 30 meter lines placed parallel to the slope at three representative sites in each stand studied.

Though our method has the advantage of allowing one to sample production over a series of years simultaneously, the following problems should be recognized:

1. The trees were not sampled randomly because some trees could not be climbed.

2. Shoots could not be sampled randomly because some were in inaccessible parts of the crown.

. Heavy bearing shoots may have been absent or ndersampled due to animal predation. Trees aided by black bears (Ursus americanus), ecognizable by claw marks and broken branches, ere therefore not sampled. Less easily avoided ere the effects of red squirrels (Tamiasciurus udsonicus) who commonly cut leader shoots from he trees (Schmidt and Shearer 1971).

. On the other hand, shoots bearing cones at the ime of sampling are also apparent to man and are ikely to be over sampled; this may compensate for nderestimation due to predation.

. Estimates of the coming cone crop will be high f significant numbers of immature cones abort compare with Allen 1941, Finnis 1953, and Sarvas 962); cone numbers predicted for 1977 were not significantly higher than the actual crop--as they ould have been if abortion had been significant.

second measure of cone production was made by ounting cones which fell to the ground in three .67 x 30 M plots in each stand. Estimates of the 973 cone crop were made in 14 stands in 1974, stimates of the 1974 cone crop were made in 28 stands in 1975, and numbers of old weathered cones ere recorded in both years.

elating production to environment.--A nested nalysis of variance was used to evaluate the ffects of place and time on cone production. The nalysis detailed below determined the significance ($p<0.05$) of variation between 5 ranches in a tree, 5 trees in a stand, 6 to 16 stands in a floristically defined subassociation nd 29 stands in the entire Pinus albicaulis-accinium scoparium association. Annual variation n production was simultaneously tested as an nteraction in each nest of the analysis. The hree floristic regions included: 1. the Wind iver and Absaroka Mountains; 2. central and southwestern Montana; 3. the Bitterroot and Salmon iver Mountains (compare with Forcella 1977).

he significant effects of time detected in the receding analysis were tentatively attributed to eather. To clarify the relationship between cone ield and weather we regressed deviations of ormalized cone yields against deviations of eather variables (monthly mean temperature and monthly total precipitation) from their means in each of the 46 months preceding abscission (compare with Eis 1976). Cone yields were ormalized to eliminate the effect of large differences in average yield between stands. Regional average weather data were used (USDC 1966-1976, compare with Lowry 1966) because no data are available from Pinus albicaulis stands, because deviations in precipitation or temperature from normal at low altitude usually parallel those found at high altitude, and because regional averages should eliminate weather station peculiarities like frost pockets. Each regional weather datum summarizes the data from dozens of official weather stations.

Relating production to simple stand parameters.--Simple or multiple regressions of cone production (leader number x average leader yield, table 1) against canopy cover, tree basal area, fallen cone number, and stand size explained significant amounts of the observed variation. On the other hand, regressions of cone yield against stand age, stand area, stand elevation, stand slope-aspect, total productivity, total standing crop, and cover indicator plants either alone or in combination were never significant.

RESULTS AND DISCUSSION

Cone development.--Cone history is reviewed here as a basis for understanding our method, for relating seed production to climatic factors, and as partial explanation for within-stand tree distribution. The development of Pinus albicaulis cones occupies parts of three summers and, due to apical branch growth, evidence of progressively older cones is displayed at nodes increasingly removed from the branch tip.

1. Late in the first summer a bud develops at the branch apex.

2. Pistillate conelets emerge from these buds in the second summer about the time of snowmelt (early July); they are found in the first lateral branch whorl, are purple, are about 5 mm long, and are easily recognized. July is therefore the best month to analyze shoots to predict the two forthcoming cone crops (compare with Allen 1941). Staminate strobili mature in early July and pollination occurs at this time. By the end of the growing season (mid-September) the conelets are approximately 1.5 cm long by 0.9 cm in diameter.

3. Rapid growth begins again in July of the third summer and full size (6.3 x 4.7 cm) cones appear in the second branch whorl by mid-August. Cone maturation continues until mid-September or early October when abscission normally occurs. Undisturbed cones abscise and fall to the ground intact, but if Clark's nutcracker (Nucifraga columbiana) removes the cone scales before abscission, the cone axes may remain in lower whorls of the branch for up to 10 years (compare with Smechkin 1963). Perhaps abscission depends on a hormone produced in the cone scales shortly before abscission so that if the cones are destroyed prior to its synthesis abscission does not occur.

The cones exude and are coated with a viscous aromatic resin. The resin may reduce seed predation by squirrels (Smith 1970) and nutcrackers. It also bonds the cone scales together (Clements 1910) until the resin crystallizes or is consumed by fungi. When the cone falls from the tree, cone scales and the large wingless seeds fall away from the axis; small clusters of seedlings found on the forest floor may result either from in situ disarticulation or from animal caches (compare with Hutchins and Lanner 1982).

Table 1.--Cone crops, locations, and stand characteristics for 28 Pinus albicaulis stands

STD[1]	MTN[2]	STATE[1]	CLIM[4]	COVER[5]	SIZE[6]	AGE[7]	1976	1975	1974	1973	1972	1971	1970	1969	MEAN±SE[8]
16	WR	WY	WR	63	2	198	2.7	2.5	0.3	2.5	1.0	2.5	--	--	1.9+0.4
17	WR	WY	WR	63	1	161	2.0	3.8	1.6	1.6	1.4	1.1	--	--	1.0±0.4
18	WR	WY	WR	71	1	214	1.3	1.3	0.7	0.8	0.6	1.5	--	--	1.0±0.2
19	AB	WY	WR	63	1	131	0.7	1.7	0.2	0.9	0.9	0.7	--	--	0.9±0.2
20	AB	MT	SC	49	1	210	1.2	1.9	1.7	0.7	0.6	1.3	--	--	1.2±0.2
09	AB	MT	SC	54	2	307	0.9	1.4	1.6	1.2	1.5	0.5	0.9	--	1.1±0.2
07	BB	MT	CN	61	2	120	0.0	0.1	9.0	3.1	3.7	3.9	1.7	3.5	3.1±1.0
06	BB	MT	CN	51	3	364	0.5	0.4	2.7	1.6	1.8	2.5	0.8	1.7	1.5±0.3
08	BB	MT	CN	66	3	55	1.7	0.4	2.6	0.2	0.2	1.5	0.2	1.9	1.1±0.3
03	LB	MT	CN	66	3	132	0.2	0.0	3.8	1.8	0.5	1.3	--	--	1.3±0.6
05	CA	MT	CN	70	1	330	0.9	0.0	1.8	0.6	0.9	0.8	--	--	0.8±0.2
05	CA	MT	CN	70	1	330	0.9	0.0	1.8	0.6	0.9	0.8	--	--	0.8±0.2
04	CA	MT	CN	37	2	55	1.5	0.3	1.2	0.7	0.2	0.6	--	--	0.8±0.2
10	MD	MT	SW	52	1	205	0.6	0.8	0.7	0.2	0.6	0.9	0.2	--	0.6±0.1
01	MD	MT	SW	73	2	150	0.6	3.8	1.2	2.2	0.9	1.8	0.9	--	1.6±0.5
02	MD	MT	SW	97	2	240	1.1	4.9	5.4	4.6	3.1	4.6	1.2	--	3.6±0.7
12	EH	MT	SW	73	2	135	1.5	6.1	1.9	2.2	2.0	3.9	1.4	4.2	2.9±0.6
11	EH	MT	SW	40	3	53	0.3	2.1	0.6	0.5	0.5	1.3	0.3	1.3	0.9±0.2
14	TR	MT	SW	56	2	160	1.5	3.6	3.3	0.5	2.7	3.8	0.5	--	2.3±0.5
13	TR	MT	SW	47	2	643	0.3	0.2	0.4	0.3	1.3	0.6	0.2	--	0.5±0.1
15	BR	MT	SW	53	2	320	1.0	0.0	1.2	0.0	0.1	0.1	--	--	0.4±0.2
29	PI	MT	SW	69	3	182	1.1	2.8	8.4	2.8	6.2	3.3	0.9	3.6	3.6±0.9
22	BT	MT	WE	50	2	423	2.5	1.1	44.9	2.3	2.4	2.7	1.2	1.0	2.3±0.4
23	BT	MT	WE	18	2	29	0.5	0.8	0.5	0.8	0.8	0.3	0.1	0.1	0.5±0.1
24	BT	MT	WE	13	1	32	0.7	0.2	0.3	0.3	0.3	0.3	0.0	0.1	0.3±0.1
25	BT	MT	WE	22	2	115	0.7	3.7	0.8	3.8	1.7	1.1	0.7	0.4	1.6±0.5
26	BT	ID	NV	32	2	59	0.1	2.3	0.3	1.0	1.2	0.6	0.2	0.4	0.8±0.3
27	SR	ID	NV	30	2	94	1.1	2.6	0.8	1.9	1.1	0.7	0.3	0.5	1.1±0.3
28	SR	ID	NV	31	2	188	0.1	0.9	0.4	0.6	0.4	0.2	0.1	0.2	0.4±0.1

[1] Stand number.
[2] Mountain ranges are: Absaroka(AB), Big Belts(BB), Bitterroot(BT), Bridger(BR), Castle(CA), Elkhorn(EH), Little Belts(LB), Madison (MD), Pioneer(PI), Salmon River(SR), Tabacco River(TR), and Wind River(WR).
[3] States are: Idaho(ID), Montana(MT), and Wyoming(WY).
[4] Climate regions are: Central(CN), Northeastern Valley(NV) of Idaho, South Central(SC), Southwest(SW), Western(WE) Montana, and Wind River(WR) Wyoming.
[5] Tree canopy cover (percent).
[6] Stand size where 1=0 to 0.75 ha, 2=0.75 to 1.25 ha, and 3=1.25 ha +.
[7] Age of dominant trees.
[8] Cones per square meter.

Cone-and-seed-production.--Average stand cone production ranged from 0.3 to 3.6 cones$\cdot m^{-2}\cdot yr^{-1}$ and averaged 1.4 ± 0.2 cones$\cdot m^{-2}\cdot yr^{-1}$ (table 1). Among the 6 to 8 years studied, maximum production in different stands ranged from 2.1 to over 100 times minimum production; in the median stand maximum production was 6.5 times minimum production (table 1). The average coefficient of variation (standard deviation/mean) between years in the average stand was 0.7.

The average mature pistillate cone weighed 23 ± 7 grams (range 10 to 50 gm) with cones produced in good years tending to be larger than those produced in poor years. Average cone production ranged, then, from a minimum of 7 to an average of 32 and to a maximum of 83 gm$\cdot m^{-2}\cdot yr^{-1}$ on a ground area basis. The range observed across all years and stands was 0 to 193 gm$\cdot m^{-2}\cdot yr^{-1}$. Cone production was approximately 9 percent of total above- and belowground production in 14 stands i which total production was measured (Forcella an Weaver 1977).

The numbers of cones found on the ground were usually fewer than scars counted in tree tops. This relationship is demonstrated by the regression equation:

$$C = 0.305 + 1.314\ F$$

where C = the number of 1974 cone scars counted the treetop, F = the number of fresh cones count on the ground in 1975, and $r^2 = 0.51$. Smechkin (1963) compared similar methods in a *Pinus sibirica* forest with the same result (r^2=0.62).

Table 2.--Comparison of cone and seed crops of several Pinus forest types[1]

Forest Type	Average Cones·m^{-2}·yr^{-1}			Average Seeds·m^{-2}·yr^{-1}			Reference
	#	grams	%[3]	#	grams	#[4]	
Pinus contorta	4.7	28	--	268	0.6	2	Smith 1968, 1970
P. contorta-Purshia tridentata	4.8	24	--	120	0.4	2	Lotan 1967
P. contorta-Geranium fremontii	8.0	40	13	---	---	-	Moir 1972
P. contorta-Vaccinium myrtillus	8.0	40	5	---	---	-	Moir 1972
P. cortorta bolanderi	---	52	20	---	---	-	Westman and Whittaker 1975
P. sibirica	---	--	--	100	30	-	Formosof 1933
P. sibirica-Vaccinium myrtillus	0.1-2.4	--	--	---	---	-	Boichenko 1970
P. sylvestris-Calluna vulgaris	1.5	9	--	30	0.2	2	Sarvas 1962
P. sylvestris-Vaccinium myrtillus	3.0	18	--	60	0.4	2	Sarvas 1962
P. sylvestris-Oxalis acetosella	4.5	27	--	90	0.6	2	Sarvas 1962
P. monophylla-Juniperus osteosperma	0.1-1.8	2-34	--	1-26	1-9	28	Forcella unpubl.
P. edulis-Juniperus osteosperma	0.8	--	--	8	---	-	Forcella unpubl.
P. cembroides-Juniperus deppeanna	7.3	17	--	35	6	35	Forcella unpubl.
P. albicaulis-Vaccinium scoparium	0.3-3.6	6-84	10	20-250	2-25	30	Forcella and Weaver 1977

1 Masses of seeds and cones not provided by the author were taken from Schopmeyer (1974).

2 Ranges in figures represent smallest and largest data provided.

3 Percent total productivity except third and fourth forest types which are percent aboveground productivity only.

4 Percent total cone mass.

Je attribute the deficiency of cones found on the ground (about 25 percent) to Clark's nutcracker, squirrel, and bear activity.

Typical cones contain about 75 ± 28 seeds, each weighing 0.1 ± 0.02 gm dry. Seed live weights are about 0.17 gm (Schopmeyer 1974). Seed mass usually comprises 30 percent of cone mass and may comprise 50 percent in an especially good cone year; the proportion of cone mass devoted to seeds in other conifers is usually lower (Smith 1970 and table 2). Average seed production ranged, then, from a minimum of 2.3 to an average of 10.5 to a maximum of 27 gm·m^{-2}·yr^{-1}, i.e., from 23 to 105 to 270 seeds·m^{-2}·yr^{-1}. The range observed across all years and stands was 0-63 gm·m^{-2}·yr^{-1} and 0-630 seeds·m^{-2}·yr^{-1}. Seed production was about 3 percent of total arboreal production in 14 stands studied intensively (Forcella and Weaver 1977a). Of the approximately 75 scales on a typical cone, one third, mostly apical and basal scales, were infertile.

Comparison of Pinus albicaulis forests with other pine forests (table 2), leads to the following conclusions: Pinus albicaulis forests produce normal cone crops (32 gm·m^{-2}·yr^{-1} average). Because the cones are heavy, cone numbers are relatively small (1.4 cones·m^{-2}·yr^{-1} average). Since a large proportion of the cone is devoted to seed, seed production is relatively high (10 gm·m^{-2}·yr^{-1} average), yet because the seeds are large, seed numbers are normal (105 m^{-2}·yr^{-1} average). The net effect is to deposit normal numbers of abnormally well provisioned seeds.

Variation in cone production potential.--Total cone production is the product of mean shoot production (=cone production potential) multiplied by the number of fertile shoots per hectare. Yet, since the density of fertile shoots in a stand may be less than optimal, the yield of the average fertile shoot may be a better index of site production potential than is the total number of

cones actually produced in the stand. In the following discussion we therefore compare production potentials across vegetational units of increasing size (trees, stands, sub-association, and the entire association) by considering a sample of branches of fixed size and ignoring the actual number of shoots producing cones.

Cone crops varied significantly between branches in 29 percent of the trees studied, and between trees in 48 percent of the stands studied, but they did not vary significantly between stands in any region or between stands in all the different regions. One might conclude:

1. that cone production varies little between branches of a tree due to identical genetics and similar mesoenvironmental conditions,

2. that it varies more between trees in a stand due to greater dissimilarity in genetics and mesoenvironmental conditions, and

3. that it differs relatively little between stands in a region due to averaging of between-tree heterogeneity in forests with relatively constant genetic and mesoenvironmental conditions.

The fact that fertile branches have similar cone production potentials throughout a region or even throughout an association supports our expectation that the average cone production of a stand is determined primarily by the number of fertile shoots per hectare and their interaction with weather conditions.

Variability in time.--In the analysis of cone production potential just discussed, the between-year effect was tested as an interaction at each level. Branch production, tree production, and stand production varied significantly between years ($p=0.05$) in 60 percent, 78 percent, and 100 percent of the cases, respectively. When all stands in the three regions were considered simultaneously there were no significant differences between years.

Variability of production in time is apparently due, in part, to internal factors. Excellent cone years (with yields one standard deviation or more above mean yield) were preceded in 20 of 29 cases by poor cone years (with yields equal to or less than the mean). Since the probability of a poor seed year so defined is 50 percent, this is a significant deviation (<0.05) from our expectation. In other species poor fruit years are also followed by good fruit years, apparently because initiating fruits cannot compete with maturing fruit for available carbohydrates during initiation and development (Kozlowski 1971). The amplitude of natural cycles in fruiting might be increased by natural selection if poor seed years preceding excellent seed years resulted in better establishment of the tree through temporarily overprovisioning previously starved-out predator populations (compare with Janzen 1971, Forcella 1980); such selection could occur only if the se[ed] predator used the subject as its principle sourc[e] of food. Other variations may not have internal causes. For example, we see no physiological or evolutionary reason for the fact that 16 of 21 excellent cone crops were preceded 4 years earli[er] by a poor cone year ($p<0.05$).

Especially poor cone years (with yields more tha[n] one standard deviation below the mean) were not significantly correlated with yields in any previous year; we therefore think a poor cone ye[ar] is more likely determined by weather rather than by internal factors.

We hypothesized that the demonstrated synchrony [of] variation in cone production within a stand and within a region is due to weather; and similarly that the lack of synchrony between regions is du[e] to differences in weather between regions. To clarify the relationship between cone yield and weather we regressed deviations of normalized co[ne] yields against deviations of weather parameters (mean temperature and total precipitation) from their means in each of the 46 months preceding cone abscission as explained under methods (compare with Eis, 1976).

Cone production was correlated with preceding weather conditions, but in no simple way (table 3); six observations follow:

1. In well-sampled regions (represented by six t[o] eight stands) correlations with temperature or rainfall significant at the 0.05 level may occur in half and correlations significant at the 0.00[1] level may occur in 20 percent of the 46 months preceding cone maturation. While significant correlations become progressively harder to dete[ct] as sample sizes decrease to two stands per climatic region, it might be possible to detect significant correlations in every month if sampl[e] sizes were increased sufficiently.

2. Though many correlations are highly significant, few explain much of the observed variation in cone yield. The average r^2 is 0.21 for precipitation and 0.20 for temperature and th[e] r^2 of correlations significant at the 0.001 leve[l] are only 0.30 for precipitation and 0.35 for temperature. Assuming that variation in regiona[l] data parallels variation in higher altitude conditions, this suggests that each of the 46 months preceding cone abscission plays a smal[l] but important part in determining yield. If fin[al] yields of P. albicaulis are, in fact, determined by a summation of everyday conditions, unique events are notably less important to yields than they are for pinyon pine (Forcella 1981).

3. Numbers of significant correlations for both temperature and precipitation are similar in the prebud, bud, pollination, and cone maturation years.

4. Forty-five percent of the significant temperature correlations and 48 percent of the significant precipitation correlations occurred i[n] winter months (November-April) when 'inactive'

Table 3.--Statistically significant relationships of cone yield to weather of the 46 months preceding cone drop in southwest Montana[1]. Correlation coefficients are presented with their signs; regressions significant at the 0.1 percent, 1 percent, and 5 percent level are indicated by a, b, and no letter respectively

Factor	Temperature				Precipitation			
Year[2]	preb	bud	juv	mat	preb	bud	juv	mat
JAN	-29				+40b		-51a	+34b
FEB		-32	+43a	+42b	-40b		-35b	+48a
MAR	+39b				-45a		+54a	
APR						+29	-31	
MAY		+45a	-30	-37b		-36b		
JUN			+50a	-26		+32	-49a	
JUL	-40b				-33			
AUG		+33			+46a	-40b		
SEP	-26							-56a
OCT			+41b		-32	+31	-31	+46a
NOV			+41b		-32	+31	-31	+46a
DEC		+32			-48a		+27	

[1] Normalized deviation of yield was regressed against deviation from average climatic data as explained in the text. Correlations for other regions were generally of similar size, sign and significance and generally showed similar seasonal distribution. They will be provided upon request.

[2] Years are those before bud formation (preb), of cone bud formation (bud), of juvenile pollinated cones (juv), and of cone maturation (mat).

rees might be assumed to be little affected. orrelations with winter precipitation could be ue to its effect on summer soil water supply. he remaining significant temperature correlations ere 20 percent in spring (May-June), 16 percent n summer (July-August) and 19 percent in fall September-October). The remaining significant recipitation correlations were 15 percent in pring, 18 percent in summer, and 19 percent in all.

. Negative correlations are slightly more common han positive correlations between cone yields and ummer (80 percent negative in July-August) and inter (57 percent negative in November-April) emperatures, as they are with spring (70 percent egative in May-June), fall (65 percent negative n September-October), and winter (62 percent egative in November-April) precipitation. We are ot ready to conclude that high temperatures and eavy precipitation lower yields.

. The fact that highly significant correlations etween yield and a given developmental period may differ in sign between different areas is consistent with the observation that year-to-year variability in cone production disappears when one averages across regions.

Our results will frustrate anyone wishing to predict future cone crops from weather data. The highly significant, but weak, correlations observed suggest that a complex physiological model would be needed to make such predictions and that its final prediction wouldn't be available until shortly before the crop matured. Similar results could be had by sampling branches in a specific stand for numbers of mature or juvenile cones and, since stands in a region behave similarly, results from a representative stand might predict regional crops reasonably.

Variability associated with easily measured stand characteristics.--The considerable variability of average cone production among stands must be caused directly by site characteristics such as climate and soils and stand characteristics such

Table 4.--Regressions relating cone production[1] to easily measured stand characteristics[2]

Regression equations.	r^2
C_a = 0.470 + 0.00032 canopy cover^2	0.42
C_a = 0.288 + 0.023 basal area	0.28
C_a = 0.812 + 0.439 fallen cones	0.32
C_a = 0.450 + 0.00023 canopy cover^2 + 0.206 fallen cones	0.46
C_a = 0.430 + 0.00032 canopy cover^2 + 0.470 stand size	0.52
C_g = 0.515 + 0.00039 canopy cover^2 + 0.734 stand size	0.49
C_p = 0.269 + 0.00011 canopy cover^2 + 0.001 stand size	0.32

1 Cone production in the average year (C_a) is expressed as cones$\cdot m^{-2} \cdot yr^{-1}$. C_g and C_p represent cone production in good and poor years respectively.

2 Units were percent of ground area for canopy cover, m^2/ha for basal area, and new plus old cones/m^2 on the ground for fallen cones. Stand size was scaled with 1 = 0 = 0.75 ha, 2 = 0.75 to 1.25 ha, and 3 = more than 1.25 ha.

as age, density, and the genetic allocation of photosynthate to reproduction. Few of these variables were studied because their measurement was too costly, time consuming, or difficult. On the other hand, correlations of average cone production with easily measured stand characteristics were tested because any strong correlations discovered would be useful for managers who wish to predict production in particular stands.

Measures of stand cover and fallen cones should be correlated with cone production since they index numbers of potentially fruiting branches and their previous fruitfulness (table 4). Canopy cover alone explained 42 percent of observed variation in cone production. Basal area only explained 23 percent of the variance, probably because branch numbers were more closely related to tree cover or circumference than cross-sectional areas. Perhaps due to uneven consumption by animals, numbers of fallen cones explained only 32 percent of the observed variation. A regression combining canopy cover and numbers of fallen cones was our second best (r^2=0.46).

Our best simple predictor of cone production (table 4, r^2=0.52) involved stand size with canopy cover. Besides explaining observed variation best, this estimator has the advantage of being least expensive to apply--both canopy cover and stand size can be estimated from aerial photos in the non-field season. The 'small stand effect' is likely due to poorer fertilization in small stands than in large ones; Sarvas (1962) observed poor pollination in Pinus sylvestris when stands were smaller than 2 ha. The fact that yields of cones in good cone years (C_g=yields greater than median yields) seem to be more affected by stand size than yields in poor cone years (C_p=yields less than in median years) suggests that other factors (probably weather), override the pollination effect in poor cone years.

Other potential estimators of stand production studied were less useful. Regression of yield against stand age, stand area, stand elevation, stand slope-aspect, productivity, biomass, and the cover of indicator plants alone showed no significant correlations. Complex combinations of these factors in multiple regressions increased attributal variability (r^2) to 60 percent but since these regressions are biologically uninterpretable they are not reported.

SUMMARY AND CONCLUSIONS

Evidence of cone production--juvenile cones, mature cones, or cone scars--located at progressively older nodes of terminal branches can be used to estimate cone yields of a branch over a 6 to 8 year period from a single observation. The product of mean branch yields, so determined, and fruiting branch density (branches per m^2) provides a measure of stand cone yield through the same period.

Average reproductive production in the 29 stands observed ranged from 0.3 to 3.6 cones$\cdot m^{-2} \cdot yr^{-1}$ and 23 to 270 seeds$\cdot m^{-2} \cdot yr^{-1}$. The coefficient of variation (SD/mean) between years for cone production in the average stand was 0.7 cones$\cdot m^{-2} \cdot yr^{-1}$. While seed numbers are comparable to those observed in other pine forests their weights were greater. Cone production comprised about 9 percent of total arboreal production.

one yield potentials varied significantly etween branches in 30 percent of the trees tudied and between trees in 48 percent of the tands studied, but never between stands.

one yields varied significantly between years in ranches, trees, and stands in a region. Some nternal control is suggested by the fact that igh-yield years usually followed low-yield ears. External control is indicated by ignificant correlations between regional weather nd cone production. These correlations suggest hat temperature and precipitation conditions ave significant, but not dominant, effects in rebud, bud, juvenile cone, and mature cone years nd all months of the year. Unique events seem ess significant, therefore, for Pinus albicaulis han for Pinus edulis (Forcella 1981).

asily measured stand characteristics are never ore than mediocre predictors of average cone roduction. Our best regressions were based on anopy cover, canopy cover with fallen cones, and anopy cover with stand size. They explained 42, 5, and 52 percent, respectively, of the observed ariation. Fortunately, the best predictor is lso least expensive to apply.

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Section 2. Cone Prediction, Collection, and Processing

CONE PREDICTION, COLLECTION, AND PROCESSING

D.G.W. Edwards

ABSTRACT: Methods of predicting the size of a cone crop and the seed yield are reviewed. The planning and methods of harvesting the crop, and the procedures for seed extraction, seed cleaning and sorting are discussed.

INTRODUCTION

The expansion of reforestation programs has created a greater focus on the problems of seed supply, particularly for specific provenances and for genetically improved seeds. Rising costs for all types of seedling production have emphasized the need for high-quality seeds.

Seed production in most conifers is periodic and intervals between good crops vary. In the years between heavy crops, few or no cones may be produced. So that seeds will always be available for forest regeneration, the forester must be able to predict a heavy crop, and must know how and when to harvest the seeds and how they must be processed. Where natural regeneration is planned, advance knowledge of a heavy crop allows for modification and timing of the logging methods, or site preparation, so that the approaching seed fall is used to the best advantage.

This paper provides a broad review of cone crop prediction, cone collection and seed processing. Crop prediction, or forecasting, is the means whereby the forest manager looks ahead, sometimes as much as one and a half years, for early signs that collectable quantities of cones may develop. Should the signals be positive, resources such as manpower, equipment and funding can be organized well ahead of the collection date. Since most conifer seeds ripen and begin to disperse in a relatively short period of time, cone collections must be carefully timed. Optimally, seeds should be mature, or nearly so, and free from insect or disease damage. Several methods of cone collection, some of them mechanized, have been developed and the most appropriate one must be chosen to suit the species, and stand and crop conditions. Cone and seed processing involves numerous steps that begin with seed extraction from dried, opened cones. In many species the seed wing must be removed before the seeds are cleaned of non-seed debris and impurities and sorted to remove empty or damaged seeds. Seedl quality has to be checked in germination tests that efficient use can be made of the seeds in the nursery, and the seeds have to be prepared and packaged for cold storage. While the concepts and methodology discussed relate principally to natural stands since these satisfy the bulk of reforestation needs both at present and for the immediate future, they can also be applied in seed orchards.

CONE CROP PREDICTION

Accurate crop predicting (or forecasting) is difficult since many factors affect the crop from its initiation to seed maturation, and these ar incompletely understood. Successful predictior are based on knowledge of the reproductive cycles of the various species which have been describe in detail for Pseudotsuga menziesii (Mirb.) Franco, Tsuga heterophylla (Raf.) Sarg., T. mertensiana (Bong.) Carr., Pinus contorta (Dougl.), Thuja plicata Donn., Chamaecyparis nootkatensis (D. Don) Spach, Picea engelmannii (Parry) and P. glauca (Moench) Voss (Allen and Owens 1972; Owens 197 Owens and Molder 1984a, 1984b, 1984c, 1984d). Predictions can be made at three main stages in the reproductive cycle: (i) the crop year before flowering, (ii) the early spring of the crop year and (iii) after flowering, when conelets are visible.

1. Predictions In The Crop Year Before Flowering

Early predictions are the most complex, since they are based on factors influencing the initiation of reproductive structures and thei development. They are also the least reliable because many factors can subsequently damage the crop, so such forecasts need periodic revision and adjustment. Such predictions are based on observations on the periodicity (frequency) of cone crops over many years, the relationships to weather conditions preceding the crops, and the formation of reproductive stuctures in winter buds.

Periodicity.--The period between good seed crops varies within and among species (table 1). Th phenomenon of alternate bearing is due to the developing crop having a negative effect on th subsequent year's crop. The reasons can be morphological as, for example, in Picea glauca Tsuga heterophylla, Thuja plicata and other trees that bear reproductive structures in terminal positions on the shoots, since these species

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not have as many available locations for flower production the year following a good crop. Thus heavy crops are followed by light ones. The effects can also be physiological, the presence of a crop in one year influencing the initiation or development of buds the following year. In species that produce flowers on the previous year's shoots, such as Abies balsamea (L.) Mill. (Morris 1951; Powell 1977) or Pseudotsuga menziesii (Owens 1969; Allen and Owens 1972), new shoots tend to be short and few flower bud primordia develop, possibly because of a lower level of available carbohydrates during the year of a heavy crop. Lee and others (1979) concluded that a high carbohydrate: nitrogen ratio favored female strobilus initiation in Pinus elliottii Engelm. The minimum period between good crops in these and several other species is therefore two years (Morris 1951; Baron 1969; Dobbs and others 1976; Powell 1977). There is also some evidence that a maturing cone crop has an effect on future crops in species with a three-year reproductive cycle, such as some pines (Wenger 1957; Lester 1967; Baron 1969; Eis 1976) either by influencing the initiation and development of reproductive primordia or by affecting the developing conelets.

A heavy current crop, therefore, can be used in many species as an indicator that the next crop will be poor. However, instances of consecutive

Table 1.--Periodicity in some western conifer species. (Source: Schopmeyer 1974)

Species	Interval between good crops (years)
bies amabilis	2-3
bies grandis	2-3
bies lasiocarpa	2-4
uniperus communis	irregular
uniperus occidentalis	--
uniperus scopulorum	2-5
arix laricina	3-6
arix lyallii	1-10
arix occidentalis	1-10
icea engelmannii	2-3
icea glauca	2-6+
icea mariana	4
icea pungens	1-3
inus banksiana	3-4
inus contorta	1
inus flexilis	2-4
inus monticola	3-7
inus ponderosa	2-5
seudotsuga menziesii	2-11
uja plicata	3-4
suga heterophylla	2-8
suga mertensiana	1-5

good cone crops have been reported in a number of species (Haig and others 1941; Fowells and Schubert 1956; Maguire 1956; Eis and others 1965; Lowry 1966; Franklin 1968; Rehfeldt and others 1971), although they are rare. In any year, wide differences in crop size between stands of the same species within a region may occur. Such events demonstrate that environmental factors may at times override the negative effects of previous seed production.

In any given year the level of seed production may vary from one species to the next, and may vary from one region to another as well as among stands within a region (Haig and others 1941; McWilliams 1950; Rowe 1955; Waldron 1965b; Franklin 1968; Bingham and Rehfeldt 1970). Within a species, Franklin (1968) observed that stand to stand variation was least in heavy or very light crop years, and greatest when cone crops were medium.

Among pines, most species flower every year, yet some species are strongly cyclic in seed production (Wright 1953; Fowells and Schubert 1956; Maguire 1956; Lester 1967; Franklin 1968; Bramlett 1972). The main reason appears to be conelet abortion which can account for between 40% and 70% of the loss of a potential crop (Wright 1953; Sarvas 1962; Snyder and Squillace 1966; Lester 1967; Wang 1970; Shearer and Schmidt 1971; Bramlett 1972). High conelet loss has been related to low temperature at the time of pollination failure (Wright 1953; Sarvas 1962; Hard 1963; Boyer 1974; Schoenike 1955), physiological causes (Wright 1953; Sarvas 1962; Wang 1970; White and others 1977) and insect damage by feeding (DeBarr and Ebel 1974; Kormanik 1974; DeBarr and Kormanik 1975; Neel and others 1979).

Weather conditions.--In different species and climatic regions initiation and development of reproductive primordia occur at different times of the growing season (Gifford and Mirov 1960; Allen and Owens 1972). This is when weather conditions have been shown to be most critical. However, in many studies correlations have been found only when the weather has had a profound negative influence on the reproductive cycle so the use of climatic conditions in forecasting may only be of use when records of previous cone crops are considered (Calvert 1979). During primordia initiation and development (i.e., during the year preceding pollination) positive responses to warm, sunny weather have been noted (Lester 1967; Rehfeldt and others 1971; Eis 1973a, 1976) in many species with a two-year reproductive cycle (table 2). Moisture deficit during this period was linked by Ebell (1967) to increased strobilus production in Pseudotsuga menziesii.

In pines, interpretation of climatic effects on seed production is complicated by the three-year reproductive cycle and interactions with physiological factors causing primordia or conelet abortion (Calvert 1979). Positive correlations with weather patterns occur in several species (table 3) but only in Pinus monticola Dougl.

Table 2.--Species in which seed production increases following a warm, sunny summer

Species	Source (Period of Observation - years)
Abies grandis	Eis 1973a (37)
Abies sibirica	Miscenko 1963 (cited by Calvert 1979)
Larix leptolepis	Yanagihara and others 1960 (49) (cited by Calvert 1979)
Picea abies	LaBastide and van Vredenburch 1970 (38)
Picea glauca	Fraser 1958 (3)
Picea mariana	Fraser 1958 (3)
Picea omorika	Maurin and others 1970
Pseudotsuga menziesii	Eis 1973a (37)
	LaBastide and van Vredenburch 1970 (38)
	Lowry 1966 (48)
Tsuga canadensis	Maurin and others 1970

have correlations been found during the critical year of primordia initiation and the conelet and crop years.

Winter buds.--Interaction between climate and physiological processes becomes evident in the number of reproductive buds in species with a two-year cycle, or in the number of conelets in pines in the fall and winter preceding cone maturity. Numbers of male buds are closely correlated with the abundance of female buds in Pseudotsuga menziesii (Silen 1967) and Pinus ponderosa Laws. (Roeser 1941) and a crop prediction method based on male buds was proposed by Silen (1967). This relationship does not hold in other species (Wright 1953; Eis and Inkster 1972). Predictions are most frequently based solely on female bud abundance, using regression techniques (Medvedev and Pal'gov 1971), sequential sampling schemes (Roe 1966; Eis and Inkster 1972; Eis 1973b), or ratios of female to vegetative buds (Allen 1941a). The accuracy of these prediction methods has varied from species to species (Eis and Inkster 1972). Poor or nil crops can be predicted with 100% accuracy while forecasting of heavy crops may only be 70%-90% accurate. In pines, surviving conelets at the beginning of the second year may be used for crop predictions (Snyder and Squillace 1966; Shearer and Schmidt 1971) provided the size of the current cone crop is considered.

The use of reproductive buds in seed crop forecasting is a more direct and reliable approach

Table 3.--Positive correlations between weather and cone production in pines

Weather variable	Species	Source (Period of observation-years)
Year of primordia initiation:		
warm spring	Pinus banksiana	Larson 1961
	Pinus ponderosa	Maguire 1956 (23)
	Pinus resinosa	Lester 1967 (15)
warm, possibly droughty summer	Pinus monticola	Eis 1976 (20)
		Rehfeldt and others 1971 (18)
	Pinus ponderosa	Daubenmire 1960
	Pinus resinosa	Lester 1967 (15)
	Pinus sylvestris	LaBastide and van Vredenburch 1970 (38)
warm, possibly wet fall	Pinus monticola	Eis 1976 (20)
		Rehfeldt and others 1971 (18)
Year of conelets:		
rain following pollination	Pinus monticola	Eis 1976 (20)
warm fall	Pinus monticola	Eis 1976 (20)
Crop year:		
warm dry spring	Pinus monticola	Eis 1976 (20)

when bud types can be positively identified (Eis 1967; Eis and Inkster 1972). Cone crop prediction based on winter bud counts is the method now used in British Columbia since detailed, illustrated descriptions of reproductive bud and cone development have been published (Canadian Forestry Service 1983) for 18 western conifers. However, counting of buds still presents practical problems since representative twigs from the upper part of the crown must be sampled (Finnis 1953). These may be obtained by climbing, by shooting off the ends of branches using a rifle, or removal from recently felled trees. In some circumstances, sampling by helicopter may be justified. Samples are more readily obtained from seed orchards. Bud examinations can be carried out in the field or in the laboratory. In addition to these detailed examinations, shoots placed in containers of water can be "forced" (i.e., the buds will continue to develop and burst to reveal whether they are male, female or vegetative) under warm, humid well-lighted conditions. This process may require two to three weeks but it will confirm any diagnosis based on bud morphology.

Reproductive bud identifications, or conelet counts in pines, are carried out far enough in advance of a developing crop to provide the forester or seed orchard manager ample time to plan for a large collection operation if a heavy crop is indicated. But there is still time for the crop to fail, so its development during the spring and summer of the crop year should be nonitored. However, if winter bud appraisals indicate a poor or nil crop, further preparations are unnecessary.

2. Predictions in Early Spring of the Crop Year

During the spring of the year in which the seed crop will mature, pollination and fertilization occur in species with a two-year reproductive cycle, while fertilization only takes place in pines. After bud burst, potential seed crops can be estimated from the abundance of developing strobili (Allen 1941a; Silen 1967; Eis and Inkster 1972). Usually, abundant megastrobili indicate a large seed crop, even in some pines (Lester 1967; Shearer and Schmidt 1971) but weather conditions before, during and after bud break may cause major losses (Wright 1953; Matthews 1963).

Date of flowering varies from species to species (Wright 1953; Ahlgren 1957; Boyer 1978) but since the relative order of flowering is usually the same from year to year (Wright 1953), poor weather will not necessarily affect all species. Strobilus development can be seriously disrupted by cold, or unusually dry weather at the time of bud burst, and megastrobili are particularly susceptible to frost damage during the receptive stage (Roeser 1942; Wright 1953; Barras and Norris 1964; Hamlett 1972; Eis and Inkster 1972; Timmis 1977). Environmental stresses during the pollination and fertilization sequences are major contributors to seed crop periodicity in many trees (Haig and others 1941). Cold weather may cause pollen cone drop in Picea abies (L.) Karst (Sarvas 1968) and P. glauca (Zasada 1971) and, in addition to or combined with moisture stress, has been known to arrest pollen development completely in Pseudotsuga menziesii (Chira 1967). Since vegetative buds and shoots are less sensitive than reproductive structures to low temperatures (Hard 1963: Zasada 1971) strobilus damage may be overlooked unless the reproductive structures themselves are examined. Rain has damaged the quantity and viability of pollen in Picea glauca (Nienstaedt 1958) and Pinus ponderosa (Turner 1956). In contrast, wet weather has been reported to have no effect on the pollen of Pinus sylvestris L. or Pseudotsuga menziesii in other studies (Sarvas 1962; Silen 1962).

Methods of prediction based on strobilus abundance include regression techniques or sequential sampling, similar to those based on reproductive buds.

3. Predictions After Flowering

Predictions of the seed crop when the developing cones are visible on the trees are the easiest to use and the most accurate. Such surveys are the preferred method of crop forecasting in Ontario (Ontario Ministry of Natural Resources 1984). These forecasts not only consider the relative abundance of maturing cones, but they also take into account the quantity and quality of seeds. They allow minimum time for organization, however.

Cone crop rating.--Most rating methods are quantitative and are intended to indicate where crops are heaviest and if they are worth collecting. One method, devised for California conifers by Baron (1963) used five ratings against which crops were compared (table 4). This was based on a system described by Fowells and Schubert (1956) whose rating classes used actual numbers of cones, the numbers varying with the species. Unfortunately, Baron introduced the terms "light," "medium" and "heavy" making the method entirely

Table 4.--Cone crop rating system for California conifers (Source: Baron 1963)

Rating Category[1/]	Definition
1 -- None	- no cones on any trees
2 -- Very light	- few cones on less than 25% of the trees
3 -- Light	- few cones on more than 25% of the trees
4 -- Medium	- many cones on 25% to 50% of the trees
5 -- Heavy	- many cones on more than 50% of the trees

1/ Cones on full-crowned trees over 30 cm d.b.h.

subjective. For example, a given number of cones, say 80-100, on Pinus monticola would probably be categorized as "many" and might indicate a heavy crop, while the same number of cones on a mature Picea glauca or Pseudotsuga menziesii tree might go unnoticed. By the same token, a thousand cones on Picea engelmanii (Parry) Engelm. might constitute "many" but would be classified as "few" on a mature Thuja plicata (Dobbs and others 1976). "Medium" and "heavy" crops (table 4, categories 4 and 5) are generally considered collectable. Despite the subjectivity, similar systems have been applied elsewhere. A method using seven rating categories is used in British Columbia, while ten rating categories are used in Alaska (Zasada and Viereck 1970) as well as in Arizona and New Mexico (Schubert and Pitcher 1973). When rating a crop, attention has to be confined to that portion of the crown expected to bear cones. In Pinus monticola and Abies spp. this is limited to the top four or five whorls of branches, whereas in Picea glauca/engelmanii and Pseudotsuga menziesii the upper two-thirds of the crown is potentially cone bearing; in Thuja plicata and Pinus contorta cones may be found over the entire crown.

Other methods based on total cone counts, as well as that of Fowells and Schubert (1956), have been developed (Haig and others 1941; Wright 1953; Franklin 1968). In most species, especially those that bear crops over a large portion of the crown, such indices are limited in value, because cone production per tree increases with age, tree diameter and crown size (Haig and others 1941; Garman 1951; Crossley 1956; Roe 1963; Waldron 1965; Lotan and Jensen 1970; Stiell 1971). They may be used, however, to estimate cone yield to determine if a collection quota can be met. One exception is Pinus strobus L. which, past a certain size, does not increase its cone bearing crown with tree size so relatively small trees produce the same crop as larger ones (Wright 1953) except at high stand densities (Garber 1970).

Waldron (1965) used a subjective cone abundance rating which was then multiplied by an estimate of the surface area of the cone bearing portion of the crown to give a cone production index in Picea glauca. In Great Britain, Seal and others (1962) recommended that for Abies spp., Pseudotsuga menziesii, Picea sitchensis (Bong.) Carr. and Pinus sylvestris, the cones visible through 6x or 8x binoculars from a distance roughly equal to the tree's height can be counted and multiplied by four to estimate the total cones on the tree. Winjum and Johnson (1962) preferred to view a Pseudotsuga menziesii tree from its south side and to count the number of cones on one branch in each whorl. The total number of cones on the tree was estimated from a mathematical equation. A more complex method was proposed by Lotan and Jensen (1970) who used regression equations involving diameter at breast height, live crown ratio, stump height, age and partial cone counts in Pinus contorta. Diameter and age were found to influence cone production in Pinus ponderosa and Pseudotsuga menziesii by Linhart and others (1979). Relationships between seed production and basal area have been found in Picea engelmannii (Roe 1967), Pinus resinosa Ait. (Roe 1964; Stiell 1971), P. palustris Mill. (Crocker 1973) and P. strobus (Garber 1970).

The most useful quantitative rating methods are based on percentages of full crop values. These methods were first described for use with broad-leaved species (Sharp 1958; Grisez 1975). They compare current fruit counts with the maximum counts ever made, and offer promise in making estimates from different sources comparable. Although they have application in research (Calvert 1979), they require more effort to appl than qualitative systems and may not be much mor advantageous for large-scale predictions.

Two common errors made in rating cone crops are counting old cones that have shed their seeds ar evaluating roadside trees which, because of thei increased exposure to sunlight, often bear a heavier crop than trees further in the stand (Dobbs and others 1976).

Filled seed counts.--Final decisions on whether o collect a crop should be based on the amount of sound seeds forming in the cones. In many species, cones will develop without pollination but no seeds will be produced (Allen 1941b; Orr-Ewing 1954; Meagher 1974) so an inspection the developing seeds is essential. Abundant pollen is required for a good seed set regardle of female strobilus production (Sarvas 1957, 19 Boyer 1974; Fechner 1979). Heavy male and fema flowering usually occur in the same year and th is reflected in a higher yield of sound seeds (Cayford 1964; Roe 1964; Sarvas 1968; Zasada an Viereck 1970; Shearer and Schmidt 1971). Good seeds may be found in relatively small areas ev in poor years, but these crops should be carefu inspected before collections are undertaken.

The most common inspection method is to slice t cones longitudinally and count the number of filled seeds so exposed. Minimum filled seed counts to set collection standards (table 5) ha been established (Buszewicz and Holmes 1956; Se and others 1965; Meagher 1974; Dobbs and others 1976) and regression equations based on such da have been developed to predict the amount of go seeds in a cone crop (Buszewicz and Holmes 1956 McLemore 1962; Calvert 1978).

Insect damage to cones and seeds, as well as th presence of disease such as cone rust, should a be evaluated since they can seriously affect se yields. In light crop years, insects and disea can destroy the entire crop. The presence of insects is often, but not always, signalled by premature browning of the cones, small holes in cone scales, accumulations of frass, pitch-like exudations, and a general disfigurement of the cone. If the cone-cutting test reveals that mo than half of the visible seeds have been affec collection is probably not worthwhile.

For Pinus contorta and other species whose con are serotinous and difficult to slice, it is easier to extract the seeds by dipping the con

able 5.--Average number (and range) of filled seeds exposed per half cone, by crop year (Source: British Columbia Ministry of Forests, Silviculture Branch 1985)

pecies	Crop year						Minimum count for collectable crop[1/]
	1980	1981	1982	1983	1984	1980-1984	
bies amabilis	9	--	10	12	--	11	8-12
	(5-12)		--	(9-12)		(5-16)	
bies grandis	--	16	14	--	--	15	12-14
		(11-24)	(12-18)		(11-24)		
arix	3	--	--	--	1	3	6
occidentalis	(1-5)				--	1-5	
icea glauca/	7	--	6	4	--	6	7
Picea engelmannii	(4-10)		(3-8)	(2-7)	--	(2-10)	
icea sitchensis	--	--	--	5	--	5	5
				(3-6)		(3-6)	
inus contorta	(see text)						20 per[2/] whole cone
inus monticola	11	11	6	--	--	10	90 per
	(7-15)	(7-13)	(4-8)			(4-15)	whole cone
seudotsuga	5	1	4	2	--	5	5
menziesii	(1-7)	--	(1-7)	--		(1-7)	
huja plicata	7	2	9	--	--	8	4-6 per
	(2-12)	(1-4)	(6-11)			(1-12)	whole cone
suga heterophylla	3	1	5	--	--	4	3
	--	(1-2)	(3-7)			(1-7)	
suga mertensiana	--	--	7	--	--	7	--
			(4-10)			(4-10)	

[1/] Figures applicable just prior to collection because insects or disease may decrease counts if there is a significant time lag between examination and collection.

[2/] Dobbs and others 1976.

riefly in boiling water then oven-drying them at 5°C for three to four hours. Extracted seeds may hen be cut or crushed to reveal a firm white egagametophytic tissue (endosperm) if they are lled. For Pinus contorta a minimum of 20 filled eds per entire cone indicates a collectable crop British Columbia (Dobbs and others 1976) but perience in Alberta suggests collectability is dicated by a count of only six to eight filled eds (Hellum and Wang 1985).

NE COLLECTION

e basic objective of any collection method is to t the cones from the tree tops and into sacks in e most efficient and safe manner without damaging ed quality. All cone collections require advance anning and organization. The larger the collection operation, the more its success depends upon aff training, especially that of the supervisors obbs and others 1976; Calvert 1985). Besides nsiderations of which species and provenances e to be targeted, cone quotas and the amount of npower, equipment and storage facilities must be lculated. These have all been reviewed by Dobbs l others (1976).

ice most reforestation seeds will continue to be rived from natural forests, stands of locally important species selected specifically for seed production purposes should be reserved. These reserved stands should be at appropriate elevation intervals in seed zones where substantial reforestation is expected to occur (Pitcher 1966; Dyer 1968; Holmes 1972; Rudolf and others 1974). All collection sites must have good access and an adequate number of well-formed trees of the required species bearing a collectable crop.

The choice of collection method is influenced by several species characteristics, such as cone shape and size, tree crown shape, and the position of the cones on the tree. The collection method must also consider whether the cones occur at the branch ends or along its length, whether they are erect or pendant, and whether old cones are persistent. Cone persistency can be either a problem, as in Larix species, or an advantage, as in Pinus contorta, since their serotinous nature allows collection of more than one year's crop at a time. Other more minor characteristics, such as the extreme pitchiness in Pinus monticola or Abies cones, and the tendency for true fir cones to disintegrate at maturity, must also be weighed. The method of collection also depends on the number of crop-bearing trees and their accessibility; scattered crop trees require a different approach from many crop trees along a road or around a

clearing. Age and height of the trees, whether they are in a sub-dominant or lower crown position, and the evenness of the canopy level, if aerial collections are contemplated, must also be considered.

1. Collection Methods

There are four general methods of cone collection: climbing, felling or topping, aerial raking and clipping, and collections from squirrel caches. The advantages and disadvantages of different cone collection methods have been compared by Cornell (1984) (table 6).

Climbing.--Climbing is the oldest traditional method. It uses few items of accessory equipment compared to other methods, and causes minimum damage to the trees, but requires trained personnel skilled in safety precautions and comfortable working at heights. A climber begins picking at the top of a tree and works his way down and around the crown, using a cone hook to pull up branches bearing cones beyond reach. Cones are usually placed in a bag hanging from the worker's safety belt. Cones should not be thrown to the ground, even in sacks. Even mature cones, especially those of Abies species, should be handled gently to avoid bruising or damage to fragile seed coats (Edwards 1982). Collection costs are minimized by climbing only those trees bearing a heavy cone crop (Goddard 1958). Individual trees should be selected on the basis of phenotype and safety criteria. Climbing for cones has been found to be productive when the crop trees are immature and tree heights are le than 15 m, the cones are medium to large, the stand is fairly open, and the crowns full, with well-spaced, sturdy branches. The species suitable for climbing include Pseudotsuga menziesii, Larix occidentalis Nutt., Pinus ponderosa and P. monticola.

Felling and topping.--Tree felling to collect cones has become common in British Columbia. Collections should be coordinated with logging clearing operations, but trees may be felled specifically for cone harvest if plans are made to recover the merchantable wood later. Felling requires experienced fallers capable of placing the trees so that the tops are readily availabl for picking. Cones should be removed from only the phenotypically best trees. For safety reasons all felling must be completed before pickers ar allowed to begin work, but picking is then faster than by climbing, and no special tools are required. Collecting from felled trees is best when the crop trees are mature, where there is good access to an adequate number of trees that are not required for future collections, and when capable fallers are available. It can be used on all species except Abies, the cones of which shatter on impact with the ground, and the method is particularly useful for winter collection of Pinus contorta cones, which are more easily detached in cold weather, provided snow does no cover the downed tops.

Table 6.--Some comparisons of cone collection methods (Source: Cornell 1985)

Method	Advantages	Disadvantages
CLIMBING	Best phenotypes selected. Cones picked when ripe. Minimum damage to trees.	High climber hazard. Picking limited to nearby roads. Staff limitation-may not reach all areas at peak ripeness.
FELLING	Faster, less expensive. Less hazard than climbing. Best phenotypes selected.	Some felling hazard. Felled trees need harvesting. Need coordination with logging. Crop trees lost to further collection. Cones need to be picked promptly once trees felled.
AERIAL	Rapid. Limited surface access required. Best phenotypes selected. Cones picked when ripe. Access to all areas. Best method for some species.	Expensive. Requires large operation and extensive planning for efficiency. High pilot hazard.
SQUIRREL CACHES	Low hazard. Requires limited staff training and little special equipment.	Limited control over seed ripening. No phenotype selection. Quotas may not be met.

f trees would not otherwise be felled, or where ubsequent utilization of the timber is not easible, tree topping may be a more suitable ethod, especially in species where cones are onfined to the uppermost crown as in Pinus onticola. Tops may be cut out with a saw by limbers, or brought down with a high-powered rifle sing soft-nosed bullets for maximum effect (Dobbs nd others 1976), or removed by aerial clipping. layton (1969) found climbing and topping Picea lauca trees, followed by stripping the cones by and, was cheaper than climbing alone. This onclusion was also reached by Calvert (1985) for icea glauca and P. mariana Mill. (Britt.). hether trees are felled or tops removed, prompt icking (within 2 or 3 days) may be necessary to orestall cone opening caused by high soil temperaures, or to prevent losses to birds and animals Stein and others 1974).

nterest in machinery for stripping cones from tops nd slash of Picea mariana and Pinus banksiana egan in Ontario in the mid-1960s (Haig 1969) and quipment has been developed which can economically trip cones, particularly in Picea mariana, even n light crops (Horton 1984). The increasing emand for tree seeds has spurred other attempts to echanize cone harvesting. The use of tree shakers as been successful with some species, especially n the southern United States, but this method annot be employed except where the terrain will llow easy access and operation of the equipment, ich as in seed orchards or some seed stands. ree shakers are most effective on species with ones that are easily detached such as Picea gelmannii, Abies grandis, Pseudotsuga menziesii Pinus ponderosa (United States Dept. riculture 1972), and can remove cones very pidly; 75% of the total cones on a Pseudotsuga nziesii tree 48 cm d.b.h. and 30 metres tall re removed in 21 seconds (United Nations Food d Agriculture Organization 1968). Shaking may effectively used on smaller cone crops that uld be uneconomic to collect by climbing ichardson 1967).

rial clipping and raking.—Technology is also ing developed for aerial collections of cones obbs and others 1977; Apt and others 1979; Hedin 83) and two systems, clipping and raking, have en approved for use in Canada. Clipping employs two-man team of a helicopter pilot and a clipper erator who is secured by harness to the aircraft d operates a hydraulic anvil-type pruner or a ecial electric chain saw. Depending upon the ecies and crown shape, either cone-laden anches or tops are removed and stored inside the rcraft as it moves from tree to tree. Aerial king uses a device, suspended below the helipter, that is lowered over the target tree until e cone bearing top protrudes through the center the cutter head. When the rake is lifted, the ad severs branches which fall into a collection sket. As with clipping, the aircraft moves from e to tree until a load has been gathered, and own to a landing for off-loading. For safety asons, pickers are permitted on the landing only en aerial delivery is complete.

Raking and clipping are suitable for use on mature trees in mixed stands when the cones are in the upper third of narrow, tapered crowns. Clipping is best used when the target trees are dominant or codominant, while raking may also be applied to lower canopy trees when they bear cones. All aerial systems require favorable weather conditions: steady winds of less that 15 kmh, and little or no rain. Both systems can be used for collecting Pseudotsuga menziesii or Picea cones. If used on other species, clipping can become prohibitively costly, but raking is ideal for true firs, and some rakes have been devised for use on Thuja plicata and Thuja heterophylla.

Aerial methods are excellent for harvesting cones from inaccessible stands, from trees in stands protecting streams, or from areas which migratory animals traverse. Because of tariff rates, equipment rentals, fuel costs, time spent training people and organizing and coordinating the collection program, aerial operations are expensive. For cost-effectiveness, both productivity and resulting seed quality must be high, which can only be achieved when there is a heavy cone crop with good seed counts. Nevertheless, the overall costs of helicopter collections have been found to be competitive (Hedin 1983; Cornell 1984), especially for species such as true firs (Wallinger 1985). Since larger quantities of cones can be harvested per day, helicopter collections can be completed in a shorter time frame, which allows them to be started closer to full ripeness of the seeds.

Squirrel caches.—Provided the source stand is of good phenotypic quality, the reforestation value of the seeds obtained from squirrel caches may not suffer unduly since caches are located in the general vicinity of the trees from which the cones are removed. Should the stand contain poor phenotypes, the method should not be used. In light crop years squirrels can seriously deplete a developing seed crop (Larson and Schubert 1970), in some instances leaving very little for the forester to collect (Shearer and Schmidt 1971). Fears that Pseudotsuga menziesii seeds from squirrel-cached cones may be of poor quality because they were cut from the trees before becoming fully mature have been dispelled by Lavender and Engstrom (1956) who observed that some cones were cut prior to full ripeness, but that the squirrels cut cones in quantity, and began caching them, only when the seeds were ripe, and that no significant increases in seed quality occurred with later cutting. Wagg (1964) observed that seed quality in cached cones of Picea glauca was higher than in cones collected from the tree because some of the mature seeds had fallen from partially opened cones on the tree, resulting in an increase in the proportion of under developed seeds in later cone collections. However, since caches are typically found in damp areas in decayed wood or duff, or around old stumps or logs, cones should be checked for the presence of pathogens. Commercial seed merchants frequently collect from caches, yet their product can be of exceptionally high quality.

2. Seed Maturation

One of the crucial considerations in any collection is that the seeds have achieved either full ripeness or a threshold of maturation from which they will continue to develop in the cones before seed extraction begins. A detailed review of seed maturation and its effects on seed quality can be found in Edwards (1980a).

While viable seeds can be obtained long before the cones are ready to open, seed maturity in conifers is usually associated with seed dispersal. Unfortunately not all the cones mature simultaneously, and calendar dates vary with locality and weather patterns. There may be variations in ripening among the cones on any one tree (Ching 1960; Fowells 1949; Maki 1940), among trees in the same stand (Allen 1958b), between different stands in the same year (Fowells 1949) and considerable variation from one collection year to another (Allen 1958a; Fowells 1949). Most conifers release their seeds quickly once maturity has been attained so the period for collecting mature seeds is no more than two weeks in most species. The general conclusion drawn from a multitude of investigations is that the more mature the seeds are when collected, the greater their vigor and potential for establishment of seedlings (Pollock and Roos 1972). Therefore the timing of seed collection has to take into account numerous considerations and if collection is delayed, even by a day or so, the bulk of the crop may be lost.

The cones of some species such as Pinus contorta, P. banksiana Lamb. and Picea mariana usually are serotinous, that is the edges of the cone scales are bonded together by resin. Cones of these species may remain intact on the tree for several years after maturation, providing a longer collection "window." In Pinus albicaulis Engelm., intact cones fall from the tree and the seeds are released only after the cones have lain on the ground and have disintegrated over several months (Krugman and Jenkinson 1974).

Among the consequences of collecting cones too early is a high moisture level that favors mold growth. Unless the cones are well ventilated during storage before seed extraction, they may suffer from heating that can cause direct damage to the seeds as well as exacerbate mold activity. The higher moisture content of immature cones requires longer kilning, thereby increasing extraction costs (Roe 1960), and normal kilning temperatures may be lethal to the immature seeds (Matyas 1973). Immature cones may fail to expand fully when kilned and remain closed or semiclosed, thus reducing seed yields (Maki 1940). Immature seeds generally do not retain their viability in storage as well as mature ones (Holmes and Buszewicz 1958), are usually lower in dry weight, may germinate slowly, are more susceptible to disease and produce a higher proportion of abnormal germinants (Edwards 1980a). Olson and Silen (1975) concluded that immature Pseudotsuga menziesii seeds collected around mid-August from a seed orchard required considerably more work to extract them from the cones and produced very light seeds. Nearly all the seeds that were collected early germinated below 10% and germin[illegible] mortality was high. They estimated that immatu[illegible] seeds cost 10 times more to produce seedlings t[illegible] seeds collected just prior to seedfall.

Maturation indices.--Numerous indices of seed maturity have been developed (Edwards 1980a). Physical indices such as cone color, seed color, cone moisture content or specific gravity, seed brittleness, and tissue shrinkage when a cut se[illegible] is exposed to the air for several hours, as wel[illegible] as chemical indices including the level of fat, sugar, starch, protein and other constituents i[illegible] the seeds have been used as indicators of the progress of ripening in many tree species, including broadleaves. Dobbs and others (1976) suggested that embryos should have extended to fill at least 75% of the cavity within the endo[illegible] sperm before cone collections are started. Embryo extension can be easily determined in the field [illegible] it can be recorded on x-ray film (Wang 1973). Recent experience has shown that early collecti[illegible] may cause germination problems in the nursery unless the cones are properly stored to allow seed ripening to be completed before the seeds are extracted. For British Columbia species it is [illegible] recommended that cone collections be delayed un[illegible] embryo extension is at least 90% complete, and until the endosperm has changed from a viscous, milky consistency to a white, firm state resembling the edible portion of a coconut (Ro[illegible] 1985). Embryo maturity is related to summer he[illegible] and in severe climates the best seeds may be fo[illegible] on southern aspects or on the south-facing side of the crowns. The utility of heat sums to predic[illegible] the time of cone collection in Pinus ponderosa [illegible] been discussed by Tanaka and Cameron (1979). Degree-day summations for judging seed maturit[illegible] have been used in Scandinavia but are not wide[illegible] used in North America (Edwards 1980a).

Other characteristics that should also be checked when judging cone ripeness have been compiled [illegible] Wallinger (1983) for west coast conifers. An illustrated guideline for estimating when to collect seeds of some eastern species includin[illegible] Picea glauca, P. mariana, P. pungens and Pinus banksiana has been recently produced also (Ont[illegible] Ministry of Natural Resources 1984).

Artificial ripening.--Prematurely collected co[illegible] containing immature seeds, require special car[illegible] prior to seed extraction. The seeds of severa[illegible] conifers, including Pseudotsuga menziesii (Sil[illegible] 1958), Picea glauca (Zasada 1973; Edwards 1980[illegible] Winston and Haddon 1981,) Larix occidentalis (Shearer 1977), as well as several Abies speci[illegible] (Rediske and Nicholson 1965; Pfister 1966; Oli[illegible] 1974) and the major southern pines (Wakeley 19[illegible]) will continue to ripen in the cones after harv[illegible] if they are properly stored. The conditions f[illegible] successful artificial ripening remain ill-defi[illegible] but where success has been obtained in the Pac[illegible] Northwest, air temperatures between 5° and 10°[illegible] relative humidities of 65%-75%, and good air circulation around the cones have all been implicated (Edwards 1980a). In other words th[illegible] cones should be kept cool and well ventilated [illegible]

hould not dry out too quickly. Cones collected 4 o 6 weeks prior to natural seedfall have produced igh quality seeds when artificially ripened for 1 o 2 months. The earlier cones are collected, owever, the more sensitive they are to storage onditions or, conversely, the more easily seed uality can be damaged (Zasada 1973). The rovision of adequate artificial ripening facili-ies in the field raises additional problems, and xpenses, but when large collections are contem-lated, an early start might make the difference etween sufficient cones being collected and quota hortfall.

. Cone Storage in the Field

ven when cones with fully mature seeds have been arvested, seed quality can be impaired at almost very subsequent step. Cones may be transported o the processing plant immediately after harvest, ut more likely they will be assembled at a hipping depot in the field. This provides an pportunity to clean them of excessive debris hich, if it is not removed, may complicate later eed cleaning.

f the cones were wet when sacked, they can be pread out at the shipping depot and air-dried, hen resacked. Proper interim storage at the hipping depot allows the cones to "cure," that s, lose some moisture as they continue to ripen. or this, individual cone sacks should be exposed o free movement of air. Additional heating, by irect sunlight for example, and rewetting must be voided. Protection from rodent depredations may lso be required. Portable racks (Stein and thers 1974) or trestles (Dobbs and others 1976) et up in well-shaded locations, or open sheds, ome of which are portable (Wallinger 1982), can eadily provide the right conditions. Cones of ies spp. are particularly susceptible to heat uildup and molding, especially if moist when acked. They should be placed in screen-bottomed rays at the interim storage shed, or as soon as ey reach the processing plant. Fans may be equired to provide adequate ventilation. Since e cones of most conifers expand as they lose oisture, sacks should not be overfilled in the ield, otherwise the scales may acquire a set that everely impairs seed extraction (Stein and others 74; Dobbs and others 1976).

Cone Transportation

eds can be injured during transportation if the nes are freshly picked, and more so if they were cked prematurely. Allowing the cones to air dry the interim storage depot, for 4 to 6 weeks for me species, makes transportation conditions less itical. Even so, cones remain perishable. Even ter sufficient drying, travel times to the ocessing plant must be kept to a minimum, and e cones kept cool and well ventilated. The use refrigerated trucks for cone shipment is now vocated in British Columbia (Johnson 1984) and moving tops of trees in Ontario (Horton 1984). ck drivers should be informed of the perishable ure of their loads, the need for proper care, and prompt delivery of their cargo. Field collection supervisors should advise the processing plant in advance of shipments so that the necessary staff will be available for prompt unloading of the cones (Dobbs and others 1976).

5. Cone Storage at the Processing Plant

Some of the cones cannot be processed immediately because of equipment limitations, but in many cases cones are stored for a further period to ensure additional drying. Specially designed sheds are normally used for this purpose (Stein and others 1974). For most species there is a period of safe storage (table 7) and seed extraction schedules need to be prepared accordingly. Cones of several British Columbia conifers have been stored for up to 6 months without loss of seed quality (Leadem 1982), but shorter periods are preferred since there is a danger of seed mortality or germination in the cones. For example, seeds in cones of Tsuga heterophylla and Thuja plicata may germinate before they can be extracted, so these species should be scheduled for early processing. Cones of Abies spp., on the other hand, are often stored for 2 months or longer, until they have completely disintegrated and do not have to be kilned. By then the seeds will be fully ripened.

Table 7.--Safe storage periods in sacks for cones of western conifers (Source: British Columbia Ministry of Forests 1985)

Species	Storage period (months)
Abies amabilis Abies grandis Abies lasiocarpa	2-4 (in trays)
Larix occidentalis	3-5
Picea engelmannii Picea glauca Picea sitchensis	3-5
Pinus contorta	4+
Pinus flexilis Pinus monticola Pinus ponderosa	3-5
Pseudotsuga menziesii	3-5
Thuja plicata	1
Tsuga heterophylla Tsuga mertensiana	1

CONE AND SEED PROCESSING

Technically, processing includes all treatments applied from the time the cones arrive at the processing plant until the seeds are prepared for sowing in the nursery. For the purposes of this review, however, only those steps leading up to cold storage will be discussed.

Upon delivery to the plant, cone sacks are identified by seedlot and stored until scheduled for processing which begins with cone drying or kilning, continues with tumbling and dewinging, and ends with cleaning and sorting. Depending upon the species and the methods employed, up to five stages may be involved in processing extracted seeds (fig. 1).

1. Kiln Drying

The objective of kilning is to open the cones quickly without damaging seed viability, so the heat must be carefully controlled (Rietz 1941; Carmichael 1958). Usually, the scales of most cones have already begun to open, but additional drying is needed to fully flex the cones into an open position to enable maximum seed recovery. Cones should be exposed to an air flow of gradually decreasing moisture content and rising temperature up to a maximum between 40° and 50°C for most species near the end of the drying period. Rapid kilning of cones still high in moisture content removes moisture from the outer layers of the scales, which partially flex and then set in a semi-open position preventing see release. This condition is known as "case-hardening" (Edwards 1981). The risk of case-hardening is reduced if the cones have been wel cured, i.e., air-dried during storage. In addition, wet seeds exposed to high kiln temper tures at the beginning of the process would likely be scalded. If the cones were too tight packed in the sacks, full opening of the scales may not occur even if drying is slow and prolonged. In some processing plants cones may be moved from the storage sheds to a ventilated lo above the kiln where escaping heat aids the drying process. This reduces kilning time and heating costs, and minimizes the chance of seed damage (Allen 1957). Once again the importance of proper cone curing, or conditioning, between the time of harvest and the start of processing is emphasized; properly handled cones require less heat so less damage to the seeds is likely resulting in a high quality product at lower co

Various kiln schedules (Wang 1973; Schopmeyer 1974) have been designed to dry and open cones the shortest possible time without damaging see viability or causing case-hardening. Most cone in British Columbia are dried in less than 16 hours (table 8), but immature cones and those attacked by insects usually do not completely c even after extended kilning. When cone scales have fully flexed the seeds fall out easily dur tumbling and should be removed from the heat as soon as possible thereafter.

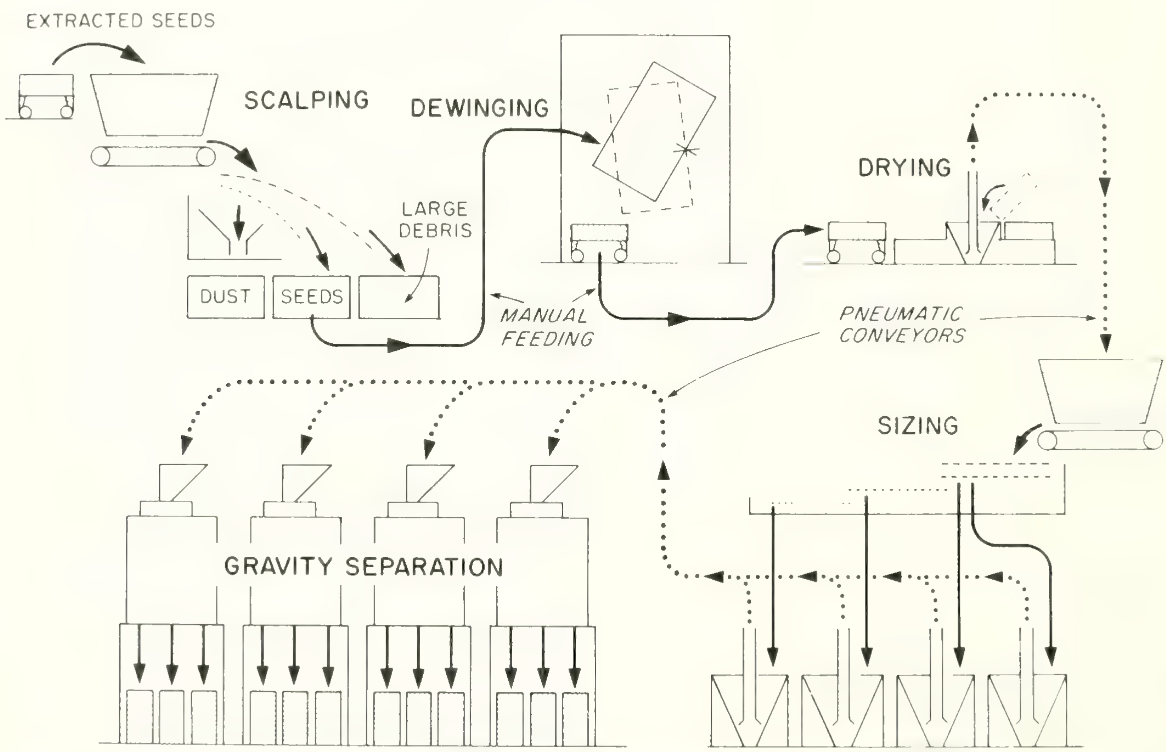


Figure 1.--The five main stages of seed processing: scalping, dewinging, drying, sizing and gravity separation. Some stages may be omitted depending upon the species and methodology. (Diagram based on the Hilleshög, Sweden, processing system which moves seeds by manual means between the early stages and pneumatic means between later stages.)

ıe outer scale edges of serotinous cones of Pinus ntorta var. latifolia are bonded together by a esin-like material, the exact nature of which is ot known (Hellum and Wang 1985), although it elts at temperatures above 45°C (Cameron 1953). widely used method for breaking the bond has en to dip the cones for about one minute in ter at 80°-90°C, after which they are kilned for veral hours at 60°C (table 8). A newer method breaking the resin bond uses a scorching device acAuley 1975) that briefly exposes cones to high mperatures. Using this process, Hellum and Wang 985) have recommended that Pinus contorta cones "cracked open" by using a flash of heat 10°-230°C for 1.5 minutes), after which they are ghtly misted with water, then kilned. A cone isture content of 15-20% at the start of kilning optimal for good seed yields regardless of the ndition of the cones up to that time (Hellum 81; Hellum and Barker 1980; Hellum and Wang 85). Most seeds are released within about 6 urs of kilning at 60°C; longer schedules crease the amount of empty seeds (Hellum 1981).

lns are essentially over-sized ovens. A basic pe consists of a large chamber equipped with aters, humidifiers and fans. Cones are spread enly on shallow trays that are stacked on vable carts or dollies. The kiln is loaded with batch of cones which are processed for the escribed time, removed when cool and a fresh tch loaded. Such kilns can process large lumes of cones at one time, but all cones in a tch are subject to the same kilning conditions. other disadvantage is that seeds that fall out the cones must remain in the kiln exposed to e high temperature until the end of the batch hedule.

some plants, kilning and tumbling are performed multaneously in a rotating drum kiln that ntains, within the heating chamber, a tumbler at shakes the seeds loose from the cones (Lowman 75). This type permits loose seeds to be moved from the heat at the earliest possible ne, but like the chamber kiln, this is also a tch-type unit. Other kilns provide continuous, -line drying by employing a tunnel along which e temperature progressively rises. Carts laden th cones on trays move slowly from the cooler trance of the tunnel to its hotter exit. A riation of this type consists of a conveyor belt which thinly spread cones move slowly through a ng heater box (Gradi 1973). Various types of lns were reviewed by Sziklai (1981). McConnell 973) described a small portable kiln designed to y small lots of pine cones featuring onomy, safety, portability and versatility.

y artificial heating involves a fire hazard and e dust, resin and dry cone scales are particu-rly inflammable (Morandini 1962; Stein and others 74). Stringent fire precautions, including a n on smoking, should be enforced, and fireproof nstruction materials should be used throughout. rangements for removal, by vacuum or other means, inflammable dust and debris are essential, and st masks should be worn by operator to reduce e health hazard.

2. Cone Tumbling

Immediately after kilning, cones are tumbled in horizontally-rotating, screened drums or cylinders to shake the seeds free. In rotating drum kilns the tumbler is programmed to revolve at intervals during the drying process so that the seeds can be removed from the heating chamber at the earliest possible time . If tumbling is delayed too long after kilning the open cones may reclose if they are exposed to moist air (Morandini 1962). During tumbling, seeds and small-sized debris fall through the drum screens into a collector or onto a conveyor belt. While some tumblers are enclosed at both ends and must be stopped for loading and unloading (Morandini 1962), more modern designs employ an open-ended, inclined cylinder. Cones are fed in at the higher end and the inclination of the drum can be altered to control the time the cones are tumbled (Turnbull 1975) so the operation can be continuous. Laboratory-sized tumblers for use in research have been described by Winjum and Ellis (1960) and Harris (1970).

Tumbling should be as brief and as gentle as possible. Prolonging the action tends to shake a higher proportion of poorly developed seeds loose and increases the amount of debris caused by cone breakage (Morandini 1962). Speed of rotation and time of tumbling must be adjusted to the cone and seed characteristics of the species. In Larix decidua Mill. and Picea abies (L.) Karst, for example, long periods of tumbling may be necessary since the seeds are frequently tightly held (Aldhous 1972).

With some species, remoistening the cones after one tumbling then redrying and additional tumbling has improved seed yields (Eliason and Heit 1940). After a first tumbling, Pinus sylvestris cones were soaked in water at 30°C for some 30 minutes, until they softened and began to reclose, and were then air-dried so that the scales opened again. The yield of seeds from the second tumbling averaged 36% of that of the first, thereby justifying the extra cost of the process (Van Haverbeke 1976). A large proportion of the seeds removed in the second tumbling are empty or poorly developed and difficult to remove in seed sorting. Seeds processed this way should be kept separate and used quickly since they may not store well (Baldwin 1942).

Some processors use screen-bottomed, tray shakers about 15-20 cm deep, the seeds falling through into a catchment bin beneath. This method is ideal for collections from seed orchards or other small lots.

3. Scalping

Following their removal from the cones, seeds are processed to remove unwanted debris, to remove the membranous wings which greatly increase their bulk and make nursery handling very difficult, and to separate empty or otherwise non-viable seeds.

Table 8.--Cone-processing schedules used in British Columbia (Source: British Columbia Ministry of Forests 1985)

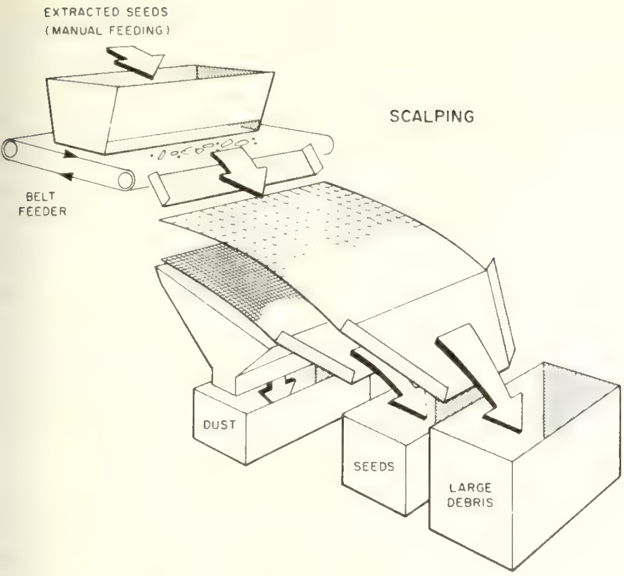
Species	Time in 80°-90°C water	Cone drying schedule: Air-drying period	Kiln-drying period: Time	Kiln-drying period: Temperature
	seconds	days	hours	°C
Abies amabilis		60-180	6-14	29-30
Abies grandis		60-180	6-14	29-30
Abies lasiocarpa		60-180	6-14	29-30
Larix laricina			8	49
Larix occidentalis			7-9	43
Picea engelmannii		20-50	6-24	38-49
Picea glauca		20-50	6-24	38-49
Picea mariana			5-11	54
Picea sitchensis		20-50	6-24	38-49
Pinus albicaulis		15-30		
Pinus contorta				
var. contorta		2-20	96	49
var. latifolia	30-60	2-30	6-8	60
Pinus flexilis		15-30	0	
Pinus monticola			14	43
Pinus ponderosa			3	49
Pseudotsuga menziesii				
Coast (var. menziesii)		8-21	2-10	32-43
Interior (var. glauca)		14-60	16-48	38-43
Thuja plicata			24-36	33
Tsuga heterophylla			16-48	30-43
Tsuga mertensiana			16-48	30-43

Immediately after tumbling the seeds still have their wings attached, and to separate them from the debris they are passed over a scalper, which consists of two or more vibrating, inclined screens, one above the other, of progressively finer mesh from the upper to the lower screen (Lowman 1975) (fig. 2). Seeds are usually retained on the intermediate screen. "Tappers" are often used to keep the particles in motion, while moving brushes under the screens reduce seed lodging in the perforations. Dust and chaff are removed by an exhaust hood.

4. Dewinging

Seedwing removal serves primarily to facilitate subsequent cleaning and to reduce the volume of material placed in cold storage and to improve the field sowing characteristics of the seedlot. In older processing plants, seed dewinging was the operational step during which seed damage through crushing, cracking or abrasion was most likely to occur (Eliason and Heit, 1940; Allen 1957; Kamra 1967; Wang 1973), but newer equipment has minimized or eliminated the danger. Excessive dewinging must be avoided since germination can be seriously damaged, the seeds seem to be more easily contaminated by mold and the resulting seedlings are weak (Baldwin 1942).

Wings are attached to the seeds by different means in different species; for example, in Pseudotsuga menziesii seeds the wing is an integral part of the seedcoat and must be mechanically broken off, while in pines and spruces the wings weakly encase the seeds and can be removed with much less abrasive action. Seeds of Abies spp. are particularly susceptible to damage to their fragile seedcoats (Edwards 1982), the reduction in viability being related to rupturing of the seed resin vesicles (Gunia and Simak 1970; Kitzmiller and others 1973, 1975). Allen (1957) observed that seeds of Abies lasiocarpa that were passed three times through a brush dewinger lost 50% of their original viability. For Abies concolor (Gord. and Gledl.) Lindl. and A. magnifica A. [illegible]



igure 2.--Seed scalping to remove particles arger and smaller than the seeds. The interhangeable screens are vibrated electromagnetially. (Diagram based on the the Hilleshög Co., weden, equipment.)

eeds, Kitzmiller and others (1975) recommended he use of a scalper treatment followed by neumatic separation as the least damaging method.

ings are small or impractical to remove from the eeds of several genera including Thuja, Cupressus, hamaecyparis and Libocedrus. Seeds of Juniperus re wingless, and since they are produced in fleshy ndehiscent strobili, commonly called "berries," uite different processing procedures must be dopted. These methods have been reviewed by tein and others (1974) and Johnsen and Alexander 1974).

ewinging methods for other conifers are generally ategorized as either dry or wet.

ry dewinging.--Dry dewinging involves rubbing the ngs off mechanically, and the simplest and safest ethod is to gently hand rub the seeds in a sack, ut this is practical for small quantities only. ne of the simplest mechanical devices is a wire reen or perforated plate, the holes of which are rge enough to allow the seeds to pass through but t the wings. A soft brush works the seeds ainst the screen while a draft of air draws off e wing fragments. Many types of mechanized wingers, mostly rotating devices, have been veloped (Lowman 1975). These may have brushes, tating knobs or paddles which force the seeds rough narrow outlets, breaking off the wings orandini 1962). Distances between the knobs, ddles, brushes and cylinder wall must be adjusted that there is neither too much pressure that uld crack or break the seedcoats nor too much iction that could cause heat damage. Lowman and savan (1978) designed a small-lot dewinger consisting of a rubber-lined, inclined cylinder with a rotating central shaft to which are attached pure gum flaps. Another type of dewinger employs a vertical cylinder inside of which is an auger that lifts and rubs the seeds against one another. Some operators add a small amount of coarse debris to enhance the rubbing action that breaks off the wings. In British Columbia this type of dewinging has proven very effective on seeds of Pseudotsuga menziesii and Larix occidentalis.

Wet dewinging.--The wings of Pinus spp. and Picea spp. are attached by means of a two-pronged depression that grips the seed (pine) or by means of a spoon-shaped hollow partially enclosing the seed (spruce). Since the wings are more hygroscopic than seeds, they expand when wet and loosen their grip on the seeds from which they can be separated cleanly with minimal agitation in a short time (Wang 1973). This is the basis of wet dewinging, a method formerly believed to impair seed quality and storability. But only a small amount of moisture is required, and since the separation process is quite rapid, the moisture content of the seeds does not increase markedly. A jet of air can be employed to blow the wings out of the mixer and simultaneously begin to redry the seeds (fig. 3).

Several types of dewingers are in use. Many are cement mixers with modified paddles, the slow rotation of which rubs the wings loose while they are lightly sprayed with water. Prolonged wetting should be avoided and it is important that the seeds be redried promptly to avoid any diminution of viability. Seeds are usually dried in a thin layer spread on fine-screened trays through which warm (<30°C) air is blown (fig. 4). It can also be carried out in a cabinet-type dryer (Lowman 1975), or a chamber-type cone kiln if it is not in use. New forced-air seed drying equipment has been developed recently in Great Britain (Waddell 1984), while a compact, multiple compartment tumbler drier was described by Leadem and Edwards (1984).

5. Seed Cleaning and Sorting

In some processing plants, seed cleaning is inseparable from sorting the better grades of seeds from incompletely developed or empty ones. After dewinging there may still be some detached wings among the seeds and further separation is required. This increases the precision with which the seeds can be mechanically sown in the nursery.

Three cleaning and sorting systems are commonly used; screens, air columns and gravity (vibrating) tables.

Screens.--One of the simplest cleaning systems is based on particle size, which is the principle of the scalper described earlier. When this is combined with an air current so that dust, chaff and light, empty seeds are blown away from the oscillating screens, the machine becomes a fanning mill. Air flow, mesh size, screen inclination,

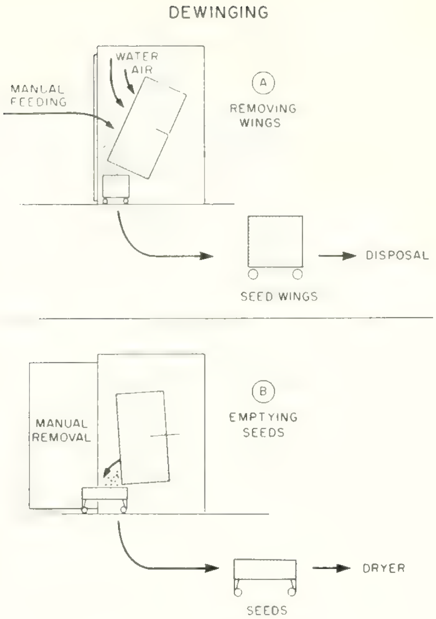


Figure 3.--Wet dewinging using a rotating barrel similar to a cement mixer. Water is added to swell the hygroscopic wings which release the seeds. An air jet blows out the loose wings and begins to redry the seeds. (Diagram based on the Hilleshög Co., Sweden, equipment.)

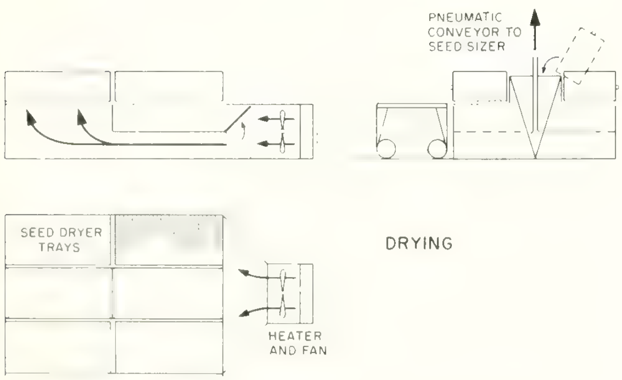


Figure 4.--Seed drying using a tray system through which warm air is forced. The drying bench is designed for easy handling of the trays. (Diagram based on the Hilleshög Co., Sweden, equipment.)

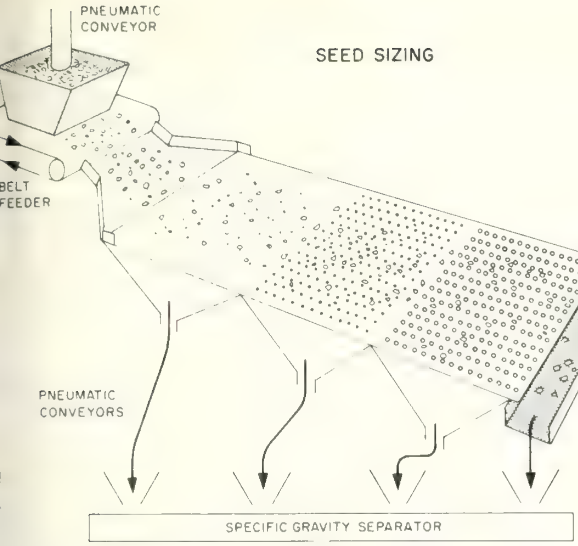
distance travelled and rate of oscillation are all usually adjustable and in some instances the fanning mill may produce the final product. For some species, or seedlots, the fanning mill is only an intermediate step and more precise cleaning has to be obtained by other means.

Air columns.--These employ a vertical air current. Separation depends on the relative rate of fall of seeds with the same surface area but different weight, or those of uniform weight but different surface area. Filled seeds sink while empty seeds are carried away by the rising air current, the velocity of which can be adjusted to suit the species. For this method to work, it is important that the seeds have been completely dewinged, since any wing remnants will increase the proportion of seeds blown away. The South Dakota blower (Erickson 1944) is one of several devices (United States Department of Agriculture 1952; Silen 1964; Hergert and others 1966; Woolard and Silen 1973; Lowman 1975; Edwards 1979) based on this principle. The efficiency of air separation is improved if the seedlot has been previously sorted into uniform size classes (fig. 5). After separation, the filled seeds from all size classes are recombined (fig. 6).

Gravity tables.--An apparatus originally developed by the mineral industry to separate ore from clay and to grade ore has been adapted by the seed industry (Lowman 1975). The specific gravity table comprises an oscillating, inclined, perforated deck, the adjustable slant and vibratory motion of which causes the seeds to move while air is forced up through the perforations, separating the seeds into layers, or strata, of different densities. Heavier particles, such as stones or dried pitch fragments "track" uphill, while the airstream "floats" lighter materials down slope. Three basic rules govern this type of sorting: a) seeds of the same size but different densities can be separated, b) seeds of different sizes but the same densities can be separated, but c) seeds of different sizes and different densities cannot be readily separated (Vaughan and others 1968; Thomas 1978). Movable dividers on the discharge edge of the table allow the seeds to be divided into a number of different density fractions. The process is rapid and efficient (Switzer 1959) and is continuous as long as the feed hopper contains seeds.

There is little evidence that gravity sorting or air separation causes seed damage, although either process might exacerbate injuries caused by other treatments. Pneumatic separation inflicted some resin vesicle damage in *Abies concolor* and *A. magnifica* seeds but it eliminated impurities and empty seeds, and was less damaging than other cleaning methods (Kitzmiller and others 1975).

Other cleaning and sorting methods for tree seeds have been described, including an inclined belt (Hergert 1971; Lowman 1975), magnetic, electrostatic, and conductivity devices (Bonner 1978; Karrfalt and Helmuth 1984), and flotation in various liquids (Baldwin 1932; McLemore 1965; Lebrun 1967; Barnett and McLemore 1970; Simak 1973; Barnett 1976). Barnett (1971) and Edwards (1980b) reported reductions in viability when organic solvents were used as seed separating agents. Attempts to use water as the separating medium were only partially successful (Edwards 1980b) until Simak (1981; 1983; 1984) described the "IDS" method. In the IDS process, seeds are soaked in water, then incubated for several days, then dried. Under the appropriate drying regime,



gure 5.--Seed sizing, shown diagrammatically
ing a single, vibrating screen with
ogressively larger perforations. Several
reens stacked vertically are typical. Each
ed-size class is then sorted separately.
iagram based on the Hilleshög Co., Sweden,
uipment.)

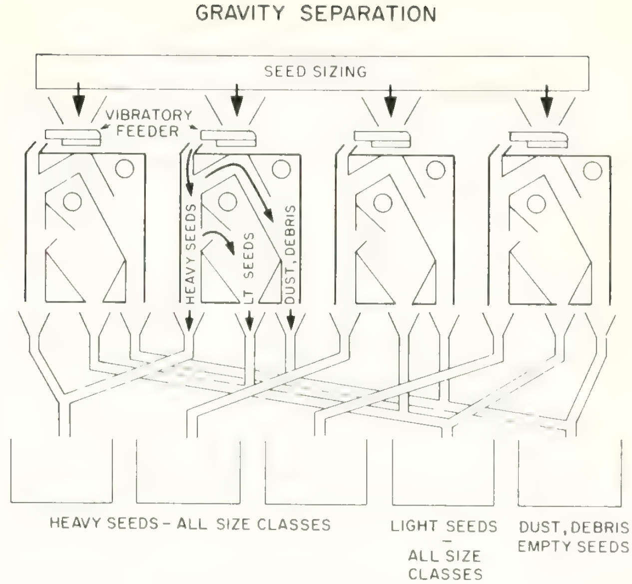


Figure 6.--Seed sorting using aspirator separators. Seeds from each size class are fed into devices from which air is drawn by vacuum. Air speed through each separator is controllable so that heavy (filled) seeds fall against the air stream while lighter seeds are drawn into a separate chamber. Dust and debris are drawn into a third chamber. Seeds from all size and weight classes are recombined. (Diagram based on the Hilleshög Co., Sweden, equipment.)

able seeds retain all or most of their moisture, ile dead seeds dry out. This difference in isture content causes live seeds to sink, and ad seeds to float, when the mixture is again aced in water. Using this method, Pinus contorta eds were improved from 67% to 96% germination pacity, retaining 72% of the original seed bulk imak 1984), and from 85.0% to 92.5%, retaining .5% of the original bulk, and from 77% to 96.5%, taining 78% of the original bulk (Edwards and hers 1985). IDS processed seeds can be stored at least two years (Edwards, unpublished). The thod is being tested on other British Columbia nifers with a view to developing a procedure for e on a large scale (Edwards, unpublished).

e efficiency of all seed cleaning and sorting thods can be checked by periodically cracking or ting samples of the processed seeds. X-ray chniques (Belcher 1973; Eden 1965; Edwards 1982) e faster and less destructive. Partially filled eds should be removed since these are often a use of fungal contamination of the seedlot, ecially in pine seeds (Rowan and DeBarr 1974). er cleaning, seeds must be thoroughly mixed to ure a homogeneous seedlot, and moisture levels t be adjusted to ensure that they meet required ndards before they are placed in low temperae storage.

noted earlier, processing normally continues h seed preservation in cold storage until needed sowing in the nursery, with germination testing , in some seed plants, with preparation of the seeds for sowing. However, these topics are beyond the scope of this review. Interested readers will find that tree seed storage has been well covered by Holmes and Buszewicz (1958), Stein and others (1974) and Wang (1974), and it was the subject of a recent international symposium (Wang and Pitel 1982). Tree seed testing was thoroughly described by Bonner (1974) and the special needs for the true firs were detailed by Edwards (1982). Presowing treatments have been reviewed by Bonner and others (1974).

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CAN WE ATTAIN BRITISH COLUMBIA SEED PRODUCTION GOALS FOR INTERIOR SPRUCE?

Paul J. Birzins

RACT: The British Columbia seed production et is 4,000 viable seeds per interior spruce t per year by age 15 (15 years from grafting). 983, 10-year-old ramets produced an average 5.4 cones and 27.6 filled seeds per cone, lting in a mean filled seed production per t of 1,805. One year later production was tantially lower at 46.46 filled seeds per ramet the average number of cones per ramet was and filled seeds per cone was 4.6. Based on information, orchard location, and associated induction trials, the chances of attaining seed production target are discussed.

ODUCTION

nated cone and seed yields from grafted ramets future seedling requirements are used to rmine the size of seed orchards in the coopera- British Columbia Tree Improvement Program. ure to meet seed production targets will limit positive impact of our reforestation and tree ovement programs on the forest economy. There- , the accuracy of seed production estimates be continually updated to determine the level eed production from orchards in relationship eedling demand. If these figures are not ted, seed collections from natural stands and orchards may become out of balance with ling demand, resulting in considerable financial . For example, if seed production from the ards falls below target levels, collections natural stands will be required to reach the production goal. If orchard production is determined in time to collect seed from the ral stands or there is not a good inventory eed from the designated seed zone, the seed tfall could result in a slowdown in refores- on. This would result in a loss of desirable ies on productive growing sites, which would tually lead to a decrease in the annual vable cut for the area.

ected annual seedling requirements for British mbia (BC) indicate that interior spruces ea glauca, P. engelmannii, and their hybrids) continue to be the major reforestation species.

presented at the Conifer Tree Seed in the nd Mountain West Symposium, Missoula, MT, st 5-6, 1985.

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Recent data for the BC interior show that anticipated annual demand by the year 2000 for interior spruce will be 86.1 million seedlings (Albricht 1985). This high interior spruce seedling demand has resulted in the allocation of a major part of tree improvement funding into grafted clonal seed orchards and associated breeding activities for the species. To date about 30 ha (96 acres) of spruce seed orchards have been established.

Our spruce seed production estimates are based on extrapolation from extremely limited data. Expectations are that by age 15 (15 years from grafting) each orchard ramet should be producing an average of 100 cones with 40 filled seeds per cone for a total of 4,000 viable seeds per ramet. Relatively recent literature indicates that this estimate may be high. Ten- to 19-year-old white spruce ramets had considerably lower production of viable seeds (2,262 per ramet) but higher cone yields of 174 cones per ramet (McPherson and others 1982). The relatively small number of filled seeds per cone (13) has also been reported for black spruce (P. mariana) (McPherson and others 1982; Verheggen and Farmer 1983).

Our first clonal orchard was established at Skimikin, BC (lat. 50°47', long. 119°14') in 1979 and therefore is too young to provide meaningful seed production information. Fortunately, in 1976 G. Kiss, BC Ministry of Forests spruce breeder, established a breeding arboretum at Vernon (lat. 50°15', long. 119°14') which is located in the hot, dry Okanagan Valley. The spruce program was originally located considerably farther north (3° of latitude); however, greater strobili production was anticipated in the Okanagan Valley, and this has been confirmed (Kiss, 1978). Based on this fact, the majority of spruce seed orchards are located in the Okanagan Valley.

WHAT ARE CURRENT SEED PRODUCTION YIELDS?

To update spruce seed yield estimates, cone and seed data were collected from clones in the oldest section of the East Kootenay breeding arboretum in 1983 and 1984.

Materials and Methods

The ramets in the East Kootenay breeding arboretum located at Vernon, BC were planted at a 5.5- by 5.5-m (18- by 18-ft) spacing on an orthic black chernozem soil (Grandview Series) from 1976 through 1979. The 1.5 ha (3.7 acre) arboretum consists of 127 clones planted in clonal row plots (4 ramets per clone). Scions were collected from ortets

located between latitudes 49°01' and 50°52', longitudes 114°18' and 116°36', elevations between 854 and 2 012 m (2,800 - 6,597 ft) and grafted onto 2-year-old rootstock using the side veneer technique. The 235 ramets selected for the study were grafted from 1972 through 1974, planted in 1976, and were about 2 m (6.6 ft) tall in 1983.

Bulk collections of 10 cones per ramet were made in the fall of 1983 from those ramets that had produced a sufficient number of cones. Cones were oven dried for 12 hours at 50° to 70°C (122° to 158°F). Seed was extracted by hand, dewinged, and the filled seed fraction was determined using a single-tube South Dakota blower. A sample of filled seeds in this fraction was counted and weighed. This weight was then divided into the total seed weight to determine the total number of filled seeds. Since this figure represented 10 cones, the total weight was divided by 10 to determine the number of filled seeds per cone. The study was repeated in 1984.

Results and Discussion

In 1983 the average number of cones per ramet was 65.4 (range 0-500) and the average number of filled seeds per cone was 27.6 (range 0-89). This resulted in a mean filled seed production per ramet of 1,805, which contrasted with the significantly lower production figure of 46.46 filled seeds per ramet that occurred in 1984 when the average number of cones per ramet was 10.1 (range 0-250) and the average number of filled seeds per cone was 4.6 (range 0-20). This cone and seed production information is summarized in table 1. According to local observations, in 1983 there was good male strobili production and the cone crop was the largest since the establishment of the arboretum. The 1984 cone and pollen crop was classified as very light, using the classification criteria outlined by Dobbs and others (1976). About 97 percent of the total seed production during these 2 years occurred in 1983. Cone crops in spruce stands were of similar proportion. In 1984 at a 15-year-old East Kootenay spruce clone bank near Prince George (about 3° of latitude north of Vernon) there were absolutely no cones and in 1983 there was a medium crop. This clone ban[k] consists of ramets from the same clones as th[e] ramets used in this study. This supports the inverse relationship between cone production [an]d latitude.

As illustrated in figures 1 and 2 there was a[n] extremely unequal clonal contribution to seed

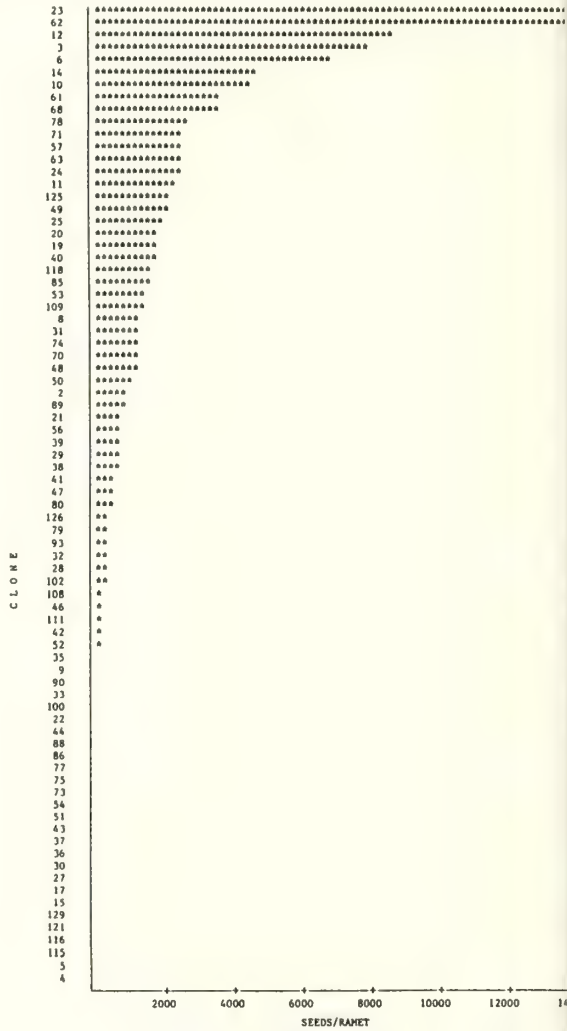
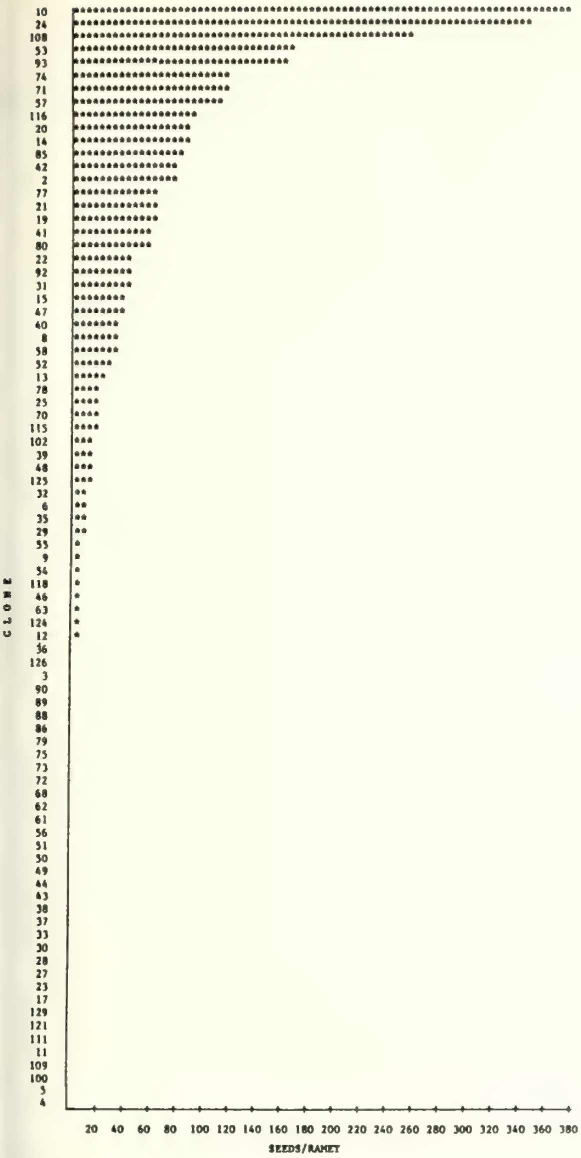


Figure 1.--Mean seed contribution per ramet b[y] clone in 1983.

Table 1.--Summary of cone and seed production from 10-year-old and 11-year-old interior spruce ramets located at Vernon, BC

Variable	10-year-old ramets (1983 data)	11-year-old ramet[s] (1984 data)
No. of clones	79	85
No. of ramets	235	235
Average no. of cones	65.4 (range 0-500)	10.1 (range 0-2[50])
Average no. of filled seed per cone	27.6 (range 0-89)	4.6 (range 0-2[0])
Mean filled seed production per ramet	1805	46.46



igure 2.--Mean seed contribution per ramet by
lone in 1984.

oduction in both the marginal and bumper crop
ars at the arboretum. The discrepancy between
onal number (79 clones in 1983 compared to 85
ones in 1984) is attributed to seed extraction
fficulties during 1983. The ANOVA for both
ars indicates significant differences in cone
oduction per clone (0.01 level). In an un-
naged seed orchard the pollen mix and cone
oduction can be very poor, as shown in the
84 data.

eally, we want equal amounts of pollen and cone
oduction per clone to maximize the genetic
ality of the seed. An unequal strobili distribu-
on per clone implies increased selfing levels
therefore decreased genetic quality. This
oblem could also be aggravated by nonsynchronous
owering in the orchard or lack of a pollen crop
significant size. Utilization of supplemental
s pollination techniques rapidly becomes an
ential orchard management tool for maximizing
quantity and quality of seed.

CONE PRODUCTION FROM TRANSPLANTED RAMETS

Our seed orchard staff has consistently observed substantial increases in spruce cone production in the year following seed orchard establishment. For instance, no cones were observed on 111 3-year-old ramets when planted at a nursery. One year after transplanting the ramets into a seed orchard, each ramet had an average of 88 cones. A similar number of ramets from the same clones that had been established in the orchard 2 years earlier had an average of only two cones per ramet.

Average heights of the two groups of ramets were quite similar (transplanted trees 134 cm [4.4 ft], orchard trees 140 cm [4.6 ft]). Obviously, transplanting accounted for the additional cone production. Eighty-one of the transplanted trees were over 100 cm (39.4 ft) tall and had an average of 14.9 cones per tree. The data from this study are summarized in table 2. With increasing size of transplanted ramets there was a pronounced increase in cone production in the year following transplanting.

DISCUSSION AND CONCLUSIONS

If the goal of 4,000 filled seeds per ramet by age 15 is to be reached, a 67 percent increase in seed production will be required in 4.5 years. The breeding arboretum is not managed as a production seed orchard; however, the cone production data suggest that unmanaged seed orchards could yield well below their biological potential. Further decreases in seed production could occur if cone and seed insects "discover" our seed orchard sites. Presently the seed orchards are isolated from natural spruce stands and are relatively free of insects and disease.

Each interior spruce cone could potentially produce about 200 seeds (Owens and Molder 1984). Up to 100 filled seeds per cone have been counted in local natural spruce stands. A conservative assumption as to the potential for filled seed production in a managed spruce seed orchard might be 90 seeds per cone. Using methods discussed by Bramlett and Godbee (1982), "seed efficiency" averaged over both the study years was only 18 percent ([16.1 seeds per cone realized - 90 seeds per cone potential] x 100). Supplemental mass pollination would be a useful tool to increase seed set.

Once we have the cones we must be able to harvest them. Flower and cone abortion losses of up to 75 percent of the crop have been observed for other species such as coast Douglas-fir (Pseudotsuga menziesii) (Bartram 1982). We don't know the magnitude of the losses for interior spruce.

In spite of the potential problems, our seed orchard managers should be able to meet our seed production goals. We know that transplanting shock substantially increases cone production. Our physiologists are attempting to duplicate these results in operational seed orchards using various combinations of root pruning, drought stressing (heat and water), GA 4/7 treatments, and fertilizing.

Table 2.--Cone production from 5-year-old transplanted interior spruce ramets

Variable	Ramets planted in 1981, data collected in 1984	Ramets planted in 19[illegible], data collected in 19[illegible]
Seed orchard planning zone	Shuswap Adams	Shuswap Adams
No. of ramets	111	111
Avg. Ht. of ramets	140 cm	134 cm
Avg. no. of cones per ramet	2	88
No. of ramets > 100 cm in ht.	101	81
Avg. cone production per ramet < 100 cm	2.198	115.07
No. of ramets ≤ 100 cm in ht.	10	30
Avg. cone production per ramet ≤ 100 cm	0	14.9

In combination with booster pollination and insect and disease control we have the potential to exceed our seed production target. With a good quantity of genetically superior seed we are off to a good silvicultural beginning.

ACKNOWLEDGMENTS

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COLD STRATIFICATION FOR LODGEPOLE PINE SEED

A. K. Hellum and I. Dymock

ABSTRACT: In this study, cold stratification did not increase total germination of immature seeds (August) of lodgepole pine, had little effect on seeds at their peak of germination (September) and elicited no or negative responses from seeds frozen in fall before fully ripe (October). The germination rate was hastened consistently by cold stratification and the 42-day treatment lead to more rapid germination than did 21 days. The need for cold stratification apparently increases again as cones and seeds remain on the tree over winter.

INTRODUCTION

Cold stratification of tree seed implies temporary storage in a moist medium at temperatures just above freezing. This allows the breaking of dormancy (Copeland 1976) so that germination can proceed. Cold stratification is also done to allow after-ripening to take place (Edwards 1980) and it is accepted that seeds absorb moisture during this time or the treatment would serve no useful purpose. Seeds that cannot take up water do not respond to moist storage or cold stratification. The stratification is usually carried out for a minimum of 15 days for north temperate pines (Krugman and Jenkinson 1974) and must, in some species, last for up to 270 days.

Some authors claim that cold stratification is not needed for the full germination of lodgepole pine (Pinus contorta Dougl. var. latifolia Engelm.) seeds from southern sources (Critchfield 1976) but it is considered as a basic need for more northern sources (Thompson 1984). It is carried out routinely on all lodgepole pine seeds used in nursery practice in Alberta. (See also Wheeler and Critchfield 1985).

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Our knowledge about what happens to seeds during cold stratification is incomplete (Tanaka 1984), but there is an understanding that if they are in need of cold stratification to germinate fully then they are not fully ripe (Edwards 1980). It is generally held that cold stratification is not harmful to germination of lodgepole pine seeds (Wang 1978).

In contrast, cold stratification normally hastens germination. The time to reach 50 percent of total germination may be shortened by days. Rapid germination in nurseries under controlled moisture conditions is a distinct advantage because it leads to the production of homogeneous crops of seedlings (Tinus and McDonald 1979). Spontaneous germination is an advantage and a requirement here, but it is certainly not desirable under variable field conditions. The need for cold stratification is therefore a built-in safety mechanism in seeds, which helps ensure that germination occurs at the right time in the field.

Cones of both spruce and pine can be collected soon after the embryo is fully developed, judging by x-ray photography, and provided the seeds are left in the cones for a month at about 10° C (50° F) and at about 65 percent relative humidity (Edwards 1978, 1980). The ripening which is taking place in such storage is therefore similar to that which takes place on the tree given that fall weather will allow this process to occur. Simak (1966), Kardell (1973), and Hellum and others (1983) have demonstrated that about 4 weeks are needed, after complete embryo development, before the seeds of Scots pine (P. sylvestris L.) and lodgepole pine reach their full germination potential.

The main purpose of this study was to test the relationship between seed ripening and the need for cold stratification. The effect of temporary cone storage before extraction was also investigated to evaluate the potential effects of after-ripening on need for cold stratification.

METHODS

The cones for this study were gathered from 20 felled trees at each of four collection times at three different altitudes (table 1) on the Procter & Gamble Cellulose (Canada) Ltd. lease area in the Grande Prairie forest of Alberta.

Table 1.--Lodgepole pine cone collections made south of Grande Prairie, Alberta, at four different times and three different altitudes between July and October 1984

Sample location	Altitude	Collection times	Total trees
	(m)		
54°55'N.,118°50'W.	670	July 17-20	80
(Lower location)		Aug 20-23	
		Sept 17-20	
		Oct 29-31	
54°38'N.,119°05'W.	970	July 17-20	80
(Middle location)		Aug 20-23	
		Sept 17-20	
		Oct 29-31	
54°25°N.,119°39'W.	1515	July 17-20	80
(Upper location)		Aug 20-23	
		Sept 17-20	
		Oct 29-31	

Cones collected in July 1984 represent the 1983 cone crop while cones collected in August to October represent the 1984 cone crop. Only trees with an estimated 30 cones or more of the desirable kind were felled. There were more trees without than with the required cones on these sites, so binoculars were used to assess each tree before felling. The 1984 cone crop was particularly poor at all three altitudes compared to 1983 and earlier crops.

Cones were kept separate by tree, site, and time of collection and seeds were extracted from 17 of the cones per tree, cleaned, and counted. The remaining cones were needed for other tests. The seeds were then pooled to make certain that the same number of filled seeds was pooled for each tree and stand per collection time. All germination tests were therefore run on fully balanced samples.

The cones were cracked open at 180° C (356° F) for about 3 minutes and then left overnight at 40° C (104° F) in a gravity vented kiln. Cones were then tumbled and seeds extracted, wet dewinged by hand, and cleaned in a North Dakota blower. The seeds were then left to air-dry for 24 hours and subsequently stored at about 3° C (37° F) until testing. Seed moisture contents were not measured after each collection trip and extraction and cleaning run because experience has shown seed moisture contents in general do not exceed 8 percent under similar conditions.

The cone moisture contents were determined within 48 hours of collection and five cones per tree, location, and collection time were dried at 105° C (221° F) for 24 hours. Moisture conditions were calculated on a dry-weight basis. Cones were dried intact without seeds being extracted first.

Eight cones were stored in paper bags in a co room kept at 5° C to 10° F (41° F to 50° F) f 7 months from time of collection to test poss effects of after-ripening on seed dormancy. weeks should be long enough to satisfy after-ripening needs after which seeds should be ab withstand drying to 5 to 7 percent moisture. Seven months were used in this study due to w pressures.

The extraction, cleaning, and counting of see took 4 weeks, and a maximum of 42 days of col stratification was used. Thus, 70 days lapse between collection and the onset of germinati tests.

Cold stratification was done between layers o moist peat at 2° C for 21 and 42 days. Four replicates of 100 seeds were first x-rayed to determine empty and damaged seed counts for a tests. They were then placed on plastic fram 22 by 22 cm (8.8 by 8.8 inches) (approximatel which were covered with Kimpak and 1 cm of mo peat moss. The seeds were spread on top of t peat in four distinct replicates. These fram were stacked one on top of the other and all covered with 2-mil plastic. These stacks, of about 20 frames, were opened only to remove f to start the germination tests or to remoiste peat every 14 days.

Dry seeds (controls) were set to germinate at same time as the 21-day and 42-day stratified seeds. The frames, Kimpak, peat, and seeds w placed in clear plastic boxes with lids and p in a Conviron germinator run at 30° C (86° F) during 8-hour days followed by 20° C(68° F) a 16-hour nights. Tests were terminated after 21st day. Tap water was added as needed in m form. The seeds were kept remarkably free of fungus or other pest problems.

Seeds were classified as germinated when the truding radicle/hypocotyl was four times the length of the seed coat. The seeds were then removed. Cutting tests were not performed af ward because all replicates were x-rayed befo tests started. Percent germination was there always calculated based on full seed only. E and damaged seed in these tests rarely exceed 5 percent. Germination was counted daily at same time.

The germination rate (R_{50}) is defined here as time needed to reach 50 percent of the total mination of a sample. It was calculated in d for each replicate, source, and collection ti by lineal interpolation on germination curves

The radiographs were taken using 20 s exposur 15 kV, 5mA (Milliampere) and a distance of 47 (18.8 inch). Seeds were put on top of the packaged film for exposing and films were the developed right away. This made it possible make sure that no replicate used had more tha about 10 percent empty or damaged seed.

RESULTS AND DISCUSSION

Cone Moisture Content

Average cone moisture contents dropped from about 60 percent of ovendry weight in mid-August to just over 20 percent in late October 1984 in all three sample stands regardless of altitude. This drying did not follow the expected concave asymptotic curve (Hellum and others 1983) observed earlier. It resembled more the right-hand part of a convex parabola showing very rapid moisture loss after rather than before the September collection (table 2). No doubt, the -20° C (-4° F) weather experienced just before the October collection affected cone ripening, but freezing tests on collected cones failed to yield useful data because the tetrazolium test was used to evaluate damages and this proved too unreliable. October was reportedly the coldest month in 30 years in Alberta.

Table 2.--Cone moisture contents for lodgepole pine at time of collection south of Grande Prairie, Alberta in 1984

Altitude of sample	Collection times (X ± 1SD)			
	July	August	September	October
(m)	1983 cones	1984 cones		
670	12.7±1.22	62.0±4.40	47.0±13.70	22.2±3.12
970	12.4±1.43	59.1±5.26	54.1± 7.18	21.8±2.56
1,515	12.8±1.44	62.5±6.09	59.3± 5.21	20.7±2.76

Natural cone drying proceeded most rapidly at the low site between August and September (15.0 percent) and slowest (3.2 percent) at the highest site. This trend was reversed between September and October. Now the cones at the highest site lost most moisture (38.6 percent) and the low site cones the least (24.8 percent). Judging by a study of 1980 cones from the same stands (Hellum and others 1983) the variability in cone moisture content should have been expected to be greatest during July and late September and least in August and in the following spring. The very rapid rates of cone drying from September to October 1984 are interpreted here as having been hastened by the -20° C (-4° F) temperatures and heavy snowfall experienced about 2 weeks before cone collection could proceed.

Coefficients of variation (table 3) suggest that tree-to-tree variability in cone moisture contents was greatest in the September collection at the low site and that August cones were quite homogeneous among trees at all altitudes. The October cones were only marginally more variable than the July cones of 1983.

The moisture contents for cones collected in July 1984, that is, cones ripened in 1983, were low (12.4 to 12.8 percent). They were between 7 and 9 percent lower than expected judging by a month-to-month survey done of cone moisture contents on the campus of the University of Alberta in 1982-1983 (Hellum unpublished). The cone moisture on campus dropped to about 15 percent in April and May in this period while it remained between 20 and 22 percent for the rest of the year. The low moisture values for July 1984 cones are interpreted as being indicative of very warm and dry forest conditions in the summer of 1984.

Table 3.--Coefficients of variation for data in table 2 on lodgepole pine cone moisture

Altitude of sample	Collection times (1984)			
	July	August	September	October
(m)	1983 cones	1984 cones		
670	9.5	7.1	20.1	14.0
970	11.5	8.9	13.3	12.1
1,515	11.2	9.7	8.8	13.3

Total Germination

Germination reached 92 percent and above for all seeds collected in September whether cold-stratified or not and regardless of location or altitude (fig. 1). The cold-stratified seeds did not reach higher levels of germination than the unstratified seeds. Seeds stratified for 42 days at 2° C (36° F) showed an average 3 percent less germination than those stratified for 21 days or not stratified at all (95 percent level of confidence).

Cold stratification at 2° C clearly damaged the high-altitude seeds collected in August (an 11.5 percent loss in total germination). The longer the cold stratification period the less germination obtained (99.9 percent level of confidence). No damages were observed in seeds collected at the mid and lower altitudes where seeds could reach 95-96 percent germination at this time.

Seeds collected in October, however, were significantly (95 percent level) less germinable (85.0 percent ± 5.5 percent) than those collected in September (95.2 percent ± 4.0 percent). Even though the seeds collected in August and September could germinate to above 90 percent the seeds collected in October never exceeded 85 percent and fell, on average, about 10 percent short of the September total. The -20° C (-4° F) temperatures in mid-October are assumed to have caused this 10 percent loss in total germination at all altitudes. It is surmised that the seeds from some trees, where cones dried more slowly, were more severely damaged than those from trees where cones had dried more rapidly (were more mature).

The cones from 1983, collected in July of 1984, showed clearly that cold stratification aided total germination in 1984 significantly (by 5 to 6 percent) at both the middle and higher altitudes (fig. 2). The trend was significant at the 99.4 percent level. The pretreatment did not influence total germination in seeds from the lower collection site. This response pattern agrees well with the 1984 cone data and the data from 1980 (Hellum and others 1983). It appears that an altitude of 670 m (2,211 ft) above sea level is low enough to allow relatively complete seed and cone ripening to occur before fall and winter frosts arrive.

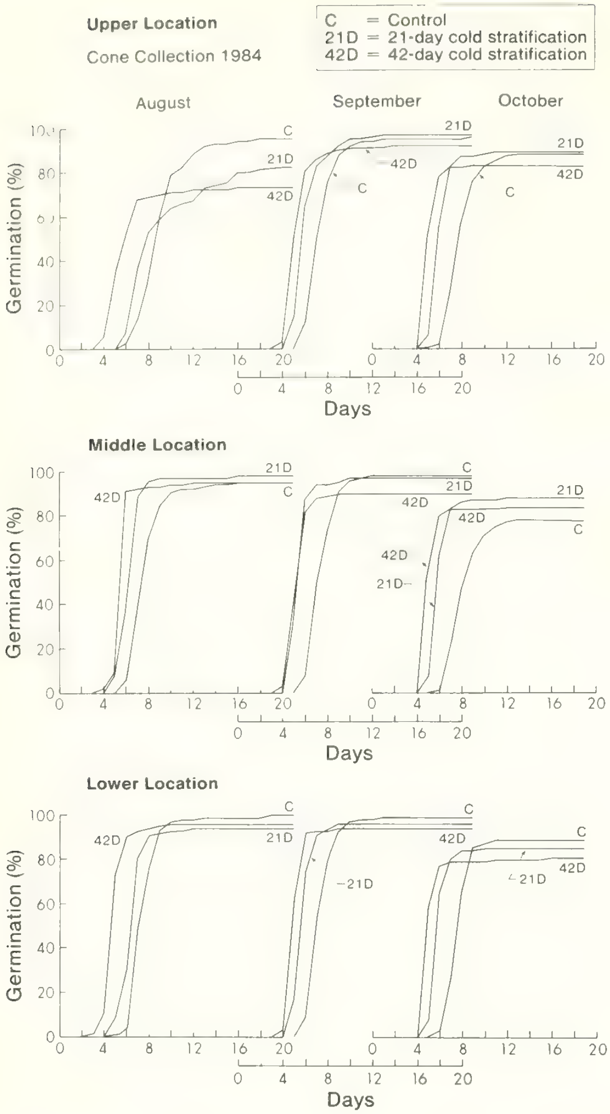

Figure 1.--Germination curves for seeds of lodgepole pine collected at three times and at three different altitudes in the Grande Prairie forest of Alberta. Seeds were cold-stratified for 21 and 42 days.

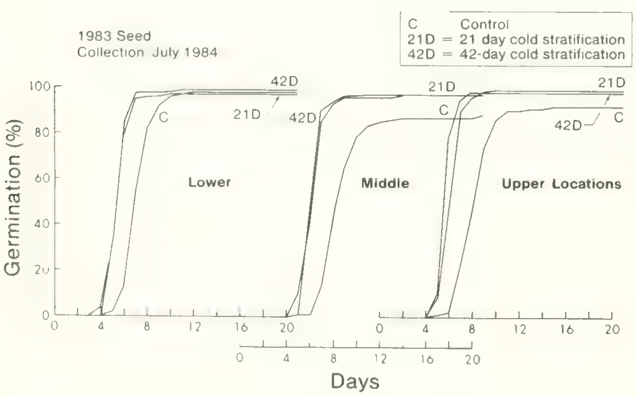

Figure 2.--Germination curves for 1983 lodgepole pine seed collected in July of 1984 from three different altitudes in the Grande Prairie forest of Alberta.

Germination Rate

Germination rates were improved significantly (99.9 percent level) with cold stratification compared to controls. The 42-day treatment gave significantly better (99.9 percent level), faster, germination (5.04 days ± 0.45) than the 21-day treatment (5.90 days ± 0.53) regardless of altitude of sample (fig. 1). The control took 7.49 days ± 0.53.

Seeds collected in September had the most rapid rate of germination (5.84 days ± 0.91), while the August seeds used 6.31 days ± 1.32 to reach the same point. The October seed was intermediate at 6.03 days ± 1.20. There was only a weak difference (significant at 90 percent level only) among germination rates over the collection period. The 1983 seeds, collected in July 1984, germinated to 50 percent in 6.40 days ± 1.03 and proved to be slower than the seeds collected in August and September, but the September seeds were similar to the October seeds (90 percent level of confidence).

The germination rate was therefore only slightly more rapid at the time when the 1984 seeds were ripest than before or after this time.

After-Ripening

Without exception, seed germination dropped significantly as a result of cone storage after August collection even though the relative humidi was maintained around 65 percent and temperatures kept at between 5 and 10° C (41 and 50° F). The attempted after-ripening led to a loss of over 31 percent germination at the lower altitude, 26.5 percent loss at the middle and 14.3 percent loss at the highest altitude site in August 1984. These losses were undoubtedly due to drying damages. A considerable proportion of the after-ripened seeds had cracked endosperms. Because after-ripening implies additional maturation such seeds should have been able to withstand long-term storage (7 months) without showing drying damages after the first 4 weeks.

The after-ripened seeds did not benefit consistently from cold stratification except in rates of germination. Total germination was sometimes

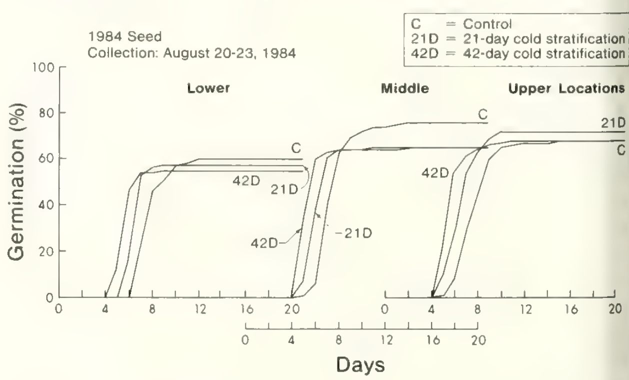

Figure 3.--Germination curves for after-ripened lodgepole pine seed collected in the Grande Prairie forest of Alberta in August of 1984.

ightly better in controls than in stratified ed and sometimes slightly worse (fig. 3). See so Winston and Haddon (1981).

NCLUSIONS

this 1-year study cold stratification hastened rmination in lodgepole pine seeds. Cold strafication also elicited three kinds of responses the same seed regarding total germination:

1. Immature (August) seeds were harmed by ld stratification at 2° C (36° F) and the nger the period of cold stratification the wer the total germination. The treatment effect s significant at the 95 percent level of confince.

2. Once the seeds had reached their peak gernation, which happened in late September in 1984, ttle or no additional germination could be tained by cold stratification. In fact, the -day stratification had a slight negative fect on germination (99.3 percent level).

3. Seeds from 1983 (collected in July of 84) benefitted by cold stratification and seeds llected in October 1984 could tolerate a 21-day riod of stratification but not a 42-day period. appears, therefore, as if seeds enter dormancy ain gradually once winter sets it. There was a ear indication in these samples that altitude ayed a role.

relative humidity of about 65 percent was not equate for maintaining necessary cone moisture ntents in order to allow after-ripening to oceed in lodgepole pine seed in this study.

KNOWLEDGMENT

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EFFECT OF STRATIFICATION TIME AND SEED TREATMENT ON GERMINATION OF WESTERN WHITE PINE SEED

R. J. Hoff

ABSTRACT: Germination of intact western white pine seeds increased from 7 percent for unstratified seeds to 83 percent for seeds that were stratified under cold-wet conditions for 15 weeks (105 days). Fifty percent of the seeds for which the seed coat and papery membrane were removed or pieces were cut away germinated with no stratification and 98 percent germinated after 15 weeks of stratification. Dormancy is determined mainly by the papery membrane and physiological elements of the embryo or gametophyte. The relative importance of these determinants changes with stratification time up to 105 days, after which only the papery membrane remains a barrier to the germination of about 15 percent of the seed. Families also had an impact on germination; family heritability of 79 percent was calculated.

INTRODUCTION

Cold-wet stratification has been the principal method for breaking dormancy in western white pine (Pinus monticola) seed. And yet high germination was seldom assured. Germination sometimes would be high, other times low; worst of all, there was no predictability even when the seed could be shown to be viable, for example by using seed cutting tests (Hoff and Steinhoff, in press).

Several kinds of treatments have been tried; for instance, alternating cold and warm stratification, acid soak, freezing, cutting, scarification, sodium hypochlorite soak, long-term soaking in water, and infrared light exposure (Larsen 1925; Anderson and Wilson 1966; Partridge and others 1985; Works and Boyd 1972; Malone 1983) have been used with variable success.

The objectives of this research were to 1) determine the effect of stratification time on germination when physiological ripeness of cones and conditions of stratification were closely controlled; 2) to assess the interactions with length of stratification of various seed treatments involving the removal of or cutting of the seed coat and papery membrane; and 3) to assess the impact of families on germination.

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METHODS AND MATERIALS

The seeds came from 20 individual trees (famili located in the Palouse River drainage, ID, latitude 46°59'N, longitude 116°33'W., elevatio 823 m (2,700 ft). Cones were harvested from individual trees when they had become flaccid--the cones were no longer hard and they could be bent back and forth with little or no crackling. In this state the cones had not dri very much, but the scales were no longer stuck each other. All cones were picked within 7 day in September 1984. Cones were dried in a greenhouse, seeds were extracted and then store at 3 °C (37 °F). Seed germination tests were started November 1984.

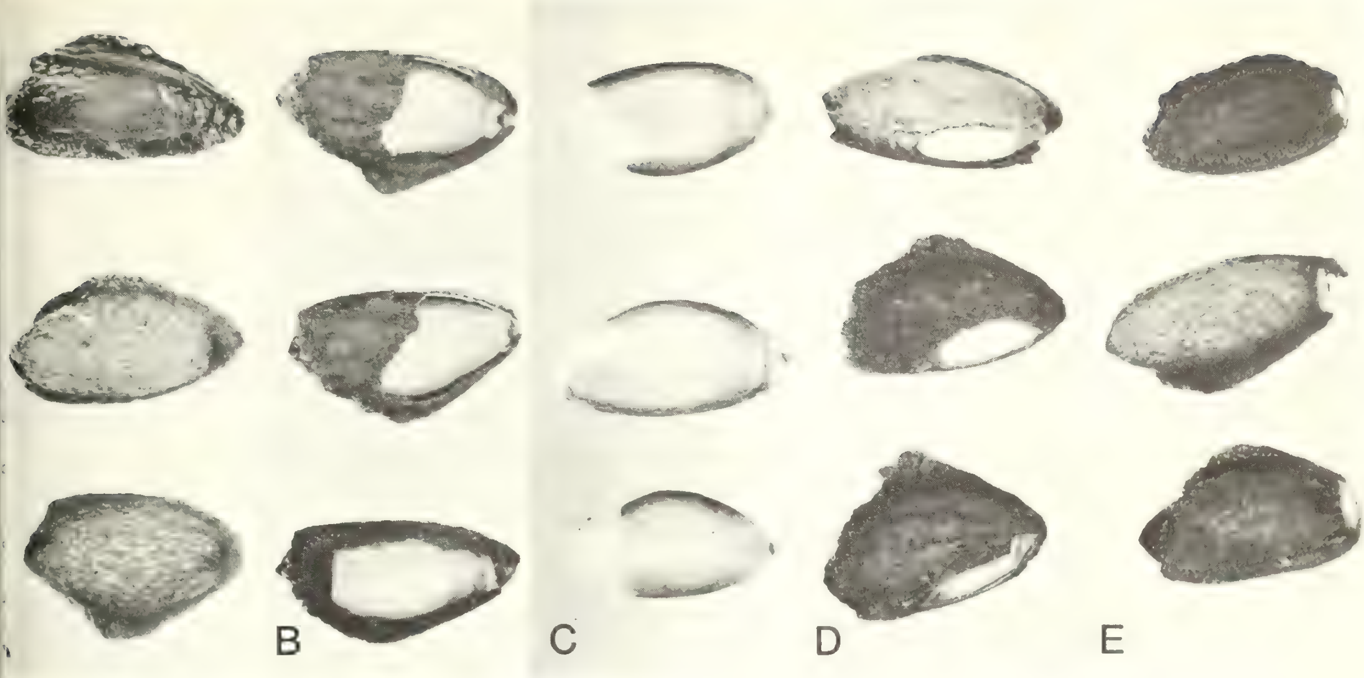
Five hundred seeds of each family were placed i a small plastic mesh bag; seed surfaces were sterilized in a 0.25 percent sodium hypochlorit solution for 10 minutes. Seeds were rinsed thr times with water and then given a 24-hour runni water rinse.

The seeds were then subjected to five seed treatments and five stratification times: 0, 21 42, 90 and 105 days.

To stratify, each of the 20 family seed lots wa rolled up in a wet paper towel and placed in an unsealed small plastic bag. An insulated box inside a refrigerator was used as a stratificat chamber and temperature was monitored remotely. Stratification temperature was maintained at 3 °C ±1 (37 °F ±1).

After each stratification time the seeds were subjected to five treatments:

1. Seeds intact (fig. 1A).
2. A part of the seed coat was carefully removed so as not to damage the membrane that lies between the seed coat and gametophyte (fig. 1B).
3. The entire seed coat was removed. Becau the membrane is attached to the seed coat at bo ends of the seed, part of the membrane was also removed (fig. 1C).
4. A slice was cut out of the seed. This c included the seed coat, membrane, and a small part of the gametophyte (fig. 1D).
5. The tip (radicle end) of the seed was cu off. This could be only 1-2 mm (1/16-inch) fro the tip so as not to cut the radicle or at least to minimize cutting it (fig. 1E).



igure 1.--Western white pine seed treatments: A, intact; B, part of the seed coat was removed leaving the apery membrane intact; C, all of the seed coat was removed which tore part of the membrane away with it; , seed was cut on the side, cutting through the seed coat, membrane, and into the gametophyte; E, the tip radicle end) was cut, cutting seed coat, membrane, and a very small piece of the gametophyte. magnification = 7x)

he seeds were incubated in 6-cm (2.4-inch) lastic petri dishes containing two filter paper ads that were kept moist. Each test was laid out n a laboratory bench maintained at 20 °C (68 °F). ermination data were taken 21 days after incubation egan. A seed was counted as a germinate when the adicle had grown at least one-half the length of he seed.

The analysis of variance and expected mean squares are shown in table 1. The model assumes that treatments are fixed and stratification time and families are random. Before analysis, the data were transformed to arcsin$\sqrt{\%}$ and differences among treatment and stratification means were determined with Duncan's New Multiple Range Test (Steel and Torrie 1960).

ible 1.--Model for analysis of variance and expected mean squares

ource of variation	Degrees of freedom	Expected mean squares[1]
lock	1	$\sigma_e^2 + tsf\sigma_b^2$
eatment (trt)	4	$\sigma_e^2 + b\sigma_{tsf}^2 + bs\sigma_{ts}^2 + bf\sigma_{ts}^2 + bsf\sigma_t^2$
ratification time (str)	4	$\sigma_e^2 + bt\sigma_{sf}^2 + btf\sigma_t^2$
milies (fam)	19	$\sigma_e^2 + bt\sigma_{sf}^2 + bts\sigma_{ts}^2$
t x str	16	$\sigma_e^2 + b\sigma_{tsf}^2 + bf\sigma_{ts}^2$
t x fam	76	$\sigma_e^2 + b\sigma_{tsf}^2 + bs\sigma_{tf}^2$
r x fam	76	$\sigma_e^2 + bt\sigma_{sf}^2$
t x str x fam	304	$\sigma_e^2 + b\sigma_{tsf}^2$
ror[2]	499	σ_e^2

here: b = 2, t = 5, s = 5, f = 20.

ontains all sources of variance involving interactions of blocks.

Table 2.--Average percentage germination of seed from 20 families of western white pine after various treatments and stratification times

	Days of cold-wet stratification					
Seed treatment	0	21	42	90	105	Mean
Intact	7	36	44	81	83	5[illegible]
Seed coat cut - membrane intact	16	33	47	81	84	5[illegible]
Seed coat removed - membrane broken	49	61	69	98	98	7[illegible]
Side of seed cut - membrane cut	50	62	77	94	99	7[illegible]
Tip of seed cut - membrane cut	51	62	71	94	99	7[illegible]
Mean	35	51	62	89	93	6[illegible]

Family heritability was calculated using the formula:

$$h^2 = \frac{\sigma_f^2}{\sigma_f^2 + \frac{\sigma_{sf}^2}{s} + \frac{\sigma_e^2}{bts}}$$

RESULTS

An increase in cold-wet stratification time resulted in an increase in germination for all seed treatments (table 2). This varied from 35 percent for no stratification over all treatments to 93 percent after 105 days' stratification. These means were significantly different at the 1 percent level of probability (table 3). Stratification time accounted for 54 percent of the variation.

Results of Duncan's New Multiple Range Test of the germination means for stratification time were:

	Stratification time				
	0 days	21 days	42 days	90 days	105 d[illegible]
$\bar{x}$ germination	35	51	62	89	9[illegible]

Means underscored by the same line are not significantly different at the 5 percent level [illegible] probability.

The effect of seed treatment is also shown in table 2. These means were significantly different at the 1 percent level of probability (table 3). Treatments accounted for 14 percent of the variation. Duncan's test at the 5 percer[illegible] level of probability indicated that treatments [illegible] and 2 (seed coat intact and membrane intact) were not significantly different and that treatments 3, 4, and 5 (those that disrupted the seed coat ar[illegible] membrane either by removal or cutting) also did not differ, but that these two groups differed.

Table 3.--Analysis of variance and variance components for percent germination of western white pine see[illegible]

Source of variance	Degrees of freedom	Mean square	Variance component	Percent of variance
Block	1	0.008	-.000	[illegible]
Treatment (trt)	4	6.881**	.033	[illegible]
Stratification time (str)	4	25.827**	.129	[illegible]
Families (fam)	19	0.675**	.012	[illegible]
Trt x str	16	0.202**	.004	[illegible]
Trt x fam	76	0.118**	.006	[illegible]
Str x fam	76	0.082**	.005	[illegible]
Trt x str x fam	304	0.056**	.010	[illegible]
Error	499	0.036	.036	[illegible]

**Statistically significant at the 1 percent level of probability.

ṛeatments 3, 4, and 5 averaged 50 percent germina-ion with no stratification compared to 12 percent or treatments 1 and 2. The differences in seed reatment decreased with stratification time. But till, at 105 days' stratification, germination of he seeds with intact coats and membranes had not qualed that of seeds whose coats and membranes ere disrupted.

eed lot also had a significant effect on germina-ion (table 3). Table 4 combines treatments 1 nd 2 and shows the frequencies of family ermination means for each stratification time. ntact seeds from two trees had more than 0 percent germination with no stratification, and here were two other trees with very low seed ermination, even after 105 days' stratification. early 100 percent of the seeds of all four of hese trees germinated after 105 days' stratifica-ion when the seed coats and membranes were isrupted.

able 5 combined treatments 3, 4, and 5 to show requencies of family germination means for each tratification time. The lowest average germination as 22 percent for no stratification and the ighest was 75 percent. After 105 days, the owest germination was 92 percent.

amily heritability was:

$$h^2_f = \frac{.012\ (.90)}{.012 + \frac{.005}{5} + \frac{.036}{50}} = .79$$

dditive genetic variation was decreased by 0 percent to account for average inbreeding in atural stands.

able 4.--Frequency of average germination by family for each stratification time for treatments 1 and 2[1]

ercent lass	Days of stratification 0	21	42	90	105
1-10	11	1	1		
1-20	7	3	2		
1-30		6	2	1	1
1-40	2	3	4		
1-50		4	3		1
1-60		3	4	1	
1-70			1	3	2
1-80			1	2	2
1-90			2	5	5
-99				5	6
100				3	3

reatment 1 = seed coat intact, reatment 2 = membrane intact.

Table 5.--Frequency of average germination by family for each stratification time for treatments 3, 4, and 5[1]

Percent class	Days of stratification 0	21	42	90	105
1-10					
11-20					
21-30	2	1			
31-40	3				
41-50	2	3			
51-60	7	4	5		
61-70	5	7	4		
71-80	1	5	4		
81-90			6	2	
91-99			1	15	7
100				3	13

[1]Treatment 3 = seed coat and part of membrane removed, treatment 4 = seed coat and membrane cut, treatment 5 = seed tip cut.

DISCUSSION

The effect of stratification time was obvious and expected. But still 105 days were not enough to overcome all the components of dormancy for the intact seed. Seeds from two trees had rather low germination (30 and 42 percent) after 105 days' stratification, and nearly every seed lot had some seed that did not germinate after 21 days' incubation. Cutting these ungerminated seeds after 21 days' incubation resulted in rapid germination. Thus, these seeds were physiologically viable.

Considering the various seed treatments together with stratification time reveals some of the "sites of dormancy." With no stratification, 7 percent of the intact seed germinated; 16 percent germinated with an intact membrane; and 50 percent of the seed with disrupted seed coat and membrane germinated. Interpretation in terms of dormancy indicates that 7 percent had no dormancy, 9 percent (16-7) had seed coat dormancy, 34 percent had dormancy due to the papery membrane (50-16), and 50 percent (100-50) had physiological elements in the embryo, gametophyte, or both, that prevented germination. Even though Duncan's test indicated that the intact seed and intact membrane treatments did not differ at all stratification times, it is possible that they do with no stratification, and thus they were kept separate. The treatments that disrupted the seed coat and membrane were averaged for each of the stratification times. Table 6 shows the proportional change of these sites of dormancy over stratification time.

Table 6.--Change in percentage of western white pine seed with no dormancy, with seed coat, membrane, and physiological dormancy for five levels of cold-wet stratification

Site of dormancy	Days of cold-wet stratification				
	0	21	42	90	105
	- - - - - - Percent - - - - - -				
None	7	35	44	81	84
Seed coat	9	0	0	0	0
Membrane	34	22	6	14	15
Physiological	50	38	28	5	1

Physiological dormancy has probably been overcome by 90 days' stratification and possibly much earlier--sometime between 42 and 90 days. Seed coat dormancy appears to be eliminated by about 21 days of stratification. Thus, the main element of dormancy that is present after 90 and 105 days involves the papery membrane.

The membrane or seed coat do not appear to be physical barriers, because seeds that are physiologically ready to germinate and that are inhibited by the seed coat/membrane will readily germinate through the seed tip (normal area for emergence of the radicle) when the seed is cut on the side. These structures are most likely to be barriers to water or gas exchange. For some trees, the seed coat/membrane is thought to be a barrier to oxygen transport (Stone 1957; Kozlowski and Gentile 1959).

That seed germination is strongly influenced by family is indicated by the high heritability. To assure equal representation of all families in a particular seed lot, seeds of each family should be kept separate, given the specific treatment needed to break dormancy, sown separately, and then combined after the seeds have germinated.

CONCLUSIONS

1. Cold-wet stratification resulted in high germination for most seed lots, but 105 days were not enough for some seed lots.
2. Disrupting the seed coat and membrane will result in moderate germination even without stratification.
3. The sites of dormancy observed were: seed coat, papery membrane, and physiological elements of the embryo, gametophyte, or both.
4. Family heritability was high (0.79) indicating a substantial genetic component.

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SEED DORMANCY IN THREE PINUS SPECIES OF THE INLAND MOUNTAIN WEST

Carole L. Leadem

STRACT: Several seed sources of Pinus bicaulis, Pinus contorta, and Pinus nticola were given various treatments to termine the degree and type of dormancy stricting germination in each species. The currence of physiological and mechanical rmancy was investigated using stratification oist chilling at 2^{o}C) and partial removal of e seedcoat. Development of embryo and metophyte tissue was assessed using X-rays. ere incomplete development was suspected, a mbination of warm (20^{o}C) and cold (2^{o}C) ratification was also employed.

ysiological dormancy, measured as the degree response to various stratification periods, s greatest in P. albicaulis and P. nticola, and least in P. contorta. Seed ats imposed significant restraints to dicle protrusion in P. albicaulis and P. nticola, but only slightly affected mination of P. contorta. Germination of P. picaulis is also commonly restricted by seed naturity due to short growing seasons found subalpine regions.

results are discussed with regard to the mancy strategies and the habitats in which h of the species is generally found.

RODUCTION

ds are said to be dormant when they are ced under conditions favourable for growth, fail to germinate. Dormancy, found in t tree seeds, is an important adaptive hanism because it ensures the survival of species by delaying germination until ditions in the external environment are ducive to active growth (Osborne 1981). expression of dormancy is under genetic trol (Naylor 1983), but it is also strongly luenced by environmental factors (Steinhoff others 1983; Rehfeldt 1983, 1985). ough variations in environment, plant ulations become physiologically specialized segments along the environmental gradient. mancy is part of the life strategy by which cies adapt to the local environment. Since most successful species are those which are most suited to a particular habitat, specializations in the manner by which dormancy is controlled result in a more successful life strategy. Control of dormancy can be exerted exogenously by physical, chemical, or mechanical means, but can also be achieved endogenously via morphological or physiological traits (Nikolaeva 1977). The type of control varies by species, even within members of the same genus.

Pinus albicaulis Engelm., Pinus contorta var. latifolia Engelm., and Pinus monticola Dougl. are three pines found primarily in mountainous areas throughout the western United States and Canada (fig. 1). P. albicaulis (whitebark pine) is a subalpine species common at high elevations growing in shallow soils on exposed slopes and rocky ridges. Climatic conditions are characterized by cool summers and cold winters with deep winter snowpack. Trees have high frost resistance but low shade tolerance (Krajina 1969; Franklin and Dyrness 1973). P. contorta (lodgepole pine) is an extremely adaptable tree which occurs in habitats from dry forest to swamp, and from lowlands to subalpine. Climatic requirements are also wide, but shade tolerance is almost nil, even in the driest habitats (Krajina 1969). It is usually considered a pioneer species, although it can be a persistent seral or climax species under certain conditions (Volland 1985). P. monticola (western white pine) is a relatively diverse species growing anywhere from mesic forests to swamps and bogs. It is found in lowlands, but is also well adapted to interior montane areas. Trees are moderately shade tolerant, but are not very frost resistant. P. monticola requires at least 50 cm precipitation in the interior and 100 cm along the coast (Krajina 1969).

Figure 1.--a; cone lengths, clockwise from left, P. monticola (13-20 cm), P. contorta (2-6 cm), and P. albicaulis (4-8 cm), b; seed lengths, left to right, P. albicaulis (8-13 mm), P. monticola (5-8 mm), and P. contorta (3-4 mm).

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The three species can occur sympatrically (Sowell and others 1982), but in zones where they coexist, such as the Abies lasiocarpa zone of Oregon and Washington, P. monticola tends to be distributed lower in the zone, whereas P. albicaulis is conspicuous higher in the zone (Franklin and Dyrness 1973). In addition to their distribution along environmental clines, there are indications that these three species have variable requirements for breaking seed dormancy (Anderson and Wilson 1966; Pitel and Wang 1980; Hellum and Wang 1985). The questions to be addressed in this study are how dormancy mechanisms vary among closely related members of the same genus, and if control of dormancy can be related to their habitat of origin.

MATERIALS AND METHODS

Pinus albicaulis Engelm.

In 1981 and 1982 P. albicaulis seeds (lots P81 and P82) were collected from a small stand of trees on Baker Mountain (latitude 49°28', longitude 115°38', elevation 2200 m) near Cranbrook, British Columbia. Seeds were X-rayed prior to treatment to remove empty seeds and to assess gametophyte and embryo development. For experiments in which they were sterilized, seeds were soaked for 5 minutes in a 4% solution of sodium hypochlorite (NaOCl), rinsed three times with deionized water, then soaked for 48 h in fresh deionized water. Cold stratification to release seeds from physiological dormancy was conducted at 2°C for either 30 or 60 days, as indicated in tables 1 and 2. Compound stratification was used to promote development and break dormancy of immature seeds. In compound stratification seeds receive 30 or 60 days warm stratification at 20°C followed by 30 or 60 days stratification at 2°C.

For germination tests seeds were incubated for 30 days at 20°C with continuous light (Pitel 1982). Four replications of 25 seeds each were used for each treatment. In instances where seeds were clipped, 1 mm of the seedcoat was cut from the radicle end just prior to incubation. Data were analyzed by Analysis of Variance and differences between treatment means were determined using Duncan's Multiple Range Test.

Imbibition studies were performed on 20-seed samples soaked in deionized water at 20° C. Water uptake was determined from the means of four samples which were weighed at 0, 1, 2, 4, 8, 24, 48, 72, and 96 h after the start of soaking. Moisture content (m.c.) on a fresh weight basis was calculated after seeds had been dried for 24 h at 105°C. Determinations were made on a total of three southern B.C. interior seed sources (including P82).

Pinus contorta Var. latifolia Engelm.

Seeds were obtained from four seed sources collected in the interior of B.C. between 1967 and 1973.

Prior to germination testing, seeds were soaked for 24 h and stratified for 3 wk at 2°C. Seeds were incubated at 30°C/20°C with 8 h light for 3 weeks. Four replications of 100 seeds were used for each treatment. Germination data were analyzed and water uptake was measured as described for P. albicaulis.

Pinus monticola Dougl.

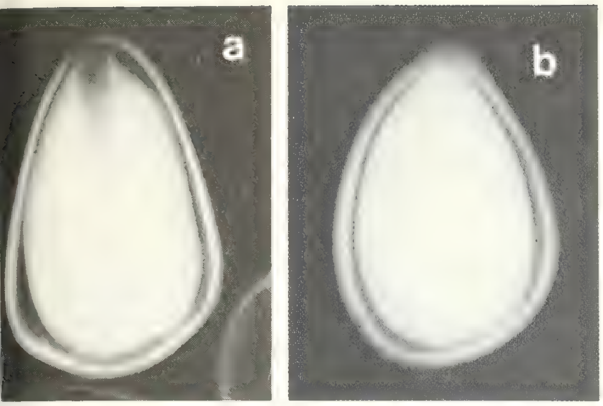
Three southern B.C. interior seed sources collected in 1964 and 1977 were used for experiments. To determine the most effective means of breaking dormancy, seeds were soaked for 24 h, then given five treatments: (1) stratification at 2°C for 60 days, (2) stratification at 2°C for 90 days, (3) stratification-redry, i.e., stratification for 30 days at 40% m.c., followed by 90 days at 30% m.c., (4) stratification for 0 days, (5) stratification for 30 days at 20°C, followed by 60 days at 2°C. To ascertain the degree of mechanical restraint imposed by the seedcoat, all stratification treatments were combined with a seedcoat treatment. Either 1 mm of the radicle end of the seed coat was cut off, or the coat was left intact. After stratification and seedcoat treatments, seeds were incubated at 30°C/20°C for 3 weeks with 8 hours light during the high temperature period. Four replications of 100 seeds were used for each treatment, and data were analyzed as for P. albicaulis. Water uptake was measured as described for P. albicaulis.

RESULTS

Pinus albicaulis

Morphological dormancy, defined by Nikolaeva (1977) as under-development of the embryo, was clearly evident in P. albicaulis. Embryo and gametophyte tissue incompletely filled the seeds prior to treatment (fig. 2a), but maintaining imbibed seeds under warm conditions for 30 to 60 days effectively promoted development of the immature tissue. This was visually demonstrated in X-rays taken following stratification (fig. 2b) and by results of germination tests (table 1).

The effects of cold temperatures on germination also indicated the presence of physiological dormancy. Warm temperatures enhanced seed development, but seeds still required an additional 60 days at 2°C to break dormancy (table 1). However, it was first necessary to remove mechanical restraint by clipping the coats, for even with the longest compound stratification, only 4% of the seeds



ure 2.--Seed development of Pinus albicaulis determined by X-ray. (a) prior to treatment after 30 days at 20°C plus 60 days at 2°C.

h intact coats were able to germinate. A h incidence of microbial growth was noted all treatments during the first test, so a ond experiment was devised to examine if face sterilization would reduce mold and s improve germination. Seeds were rilized, rinsed, and imbibed for 48 h prior receiving either 60 days cold, or 60 days n plus 60 days cold stratification. All s were clipped prior to incubation to ove mechanical restraint. Sterilization y slightly increased germination of seeds ch received cold stratification, but nificantly improved germination of seeds ch received the combined warm and cold atment (table 2). Mold was still apparent ng testing, but in view of the gains made germination, sterilization was continued as standard procedure.

ird experiment was performed to see if e was any benefit to modifying the edure by completely removing the seed . Seeds were sterilized, then stratified g the combined warm and cold treatment. r stratification, coats were either left ct, clipped, or removed. In intact seeds, ination was 8%, but both seedcoat tments resulted in higher emergence (table There was apparently no advantage to ving the coat, since germination was about regardless of whether the coat was clipped ntirely removed.

lbicaulis is a hard-coated pine seed, but s did not appear to be impermeable to r. Early water uptake was rapid, reaching m.c. within 24 h, but seeds were not fully bed even after 96 h (fig. 3).

s contorta

British Columbia sources of P. contorta germinate moderately well without tification. However, stratification lly increases both germination rate and total germination, so chilling for three weeks at 2°C is commonly recommended (International Seed Testing Association 1976).

Table 1.--Effects of clipping and stratification on germination of *Pinus albicaulis* (Lot P81)

Treatment			Germination percent
Days @ 20°C	Days @ 2°C	Clipping	
0	60	-	0.0
0	60	+	0.0
30	30	-	0.0
30	30	+	0.0
30	60	-	0.0
30	60	+	8.0[b]
60	60	-	4.2[b]
60	60	+	30.0[a]

Germination after 30 days incubation at 20°C with continuous light. None of the treatments was sterilized prior to treatment. Means with the same letter are not significantly different at p=0.05.

Table 2.--Effects of sterilization and stratification on germination of *Pinus albicaulis* (Lot P82)

Treatment				Germination percent
Days @ 20°C	Days @ 2°C	Ster.	Clip	
0	60	-	+	6.7[c]
0	60	+	+	9.9[c]
60	60	-	+	20.2[b]
60	60	+	+	31.4[a]

All seeds were clipped at the radicle end just prior to incubation. Seeds were incubated for 30 days at 20°C with continuous light. Percentages followed by the same letter are not significantly different at p=0.05.

Table 3.--Effects of the seedcoat on germination of stratified P. albicaulis seeds (Lot P82)

Treatment	Germination percent
Intact coat	8.0[b]
Clipped coat	32.2[a]
No coat	30.0[a]

All seeds were surface sterilized, then stratified for 60 days at 20°C plus 60 days at 2°C. Incubation was for 30 days at 20°C with continuous light. Means with the same letter are not significantly different at p=0.05.

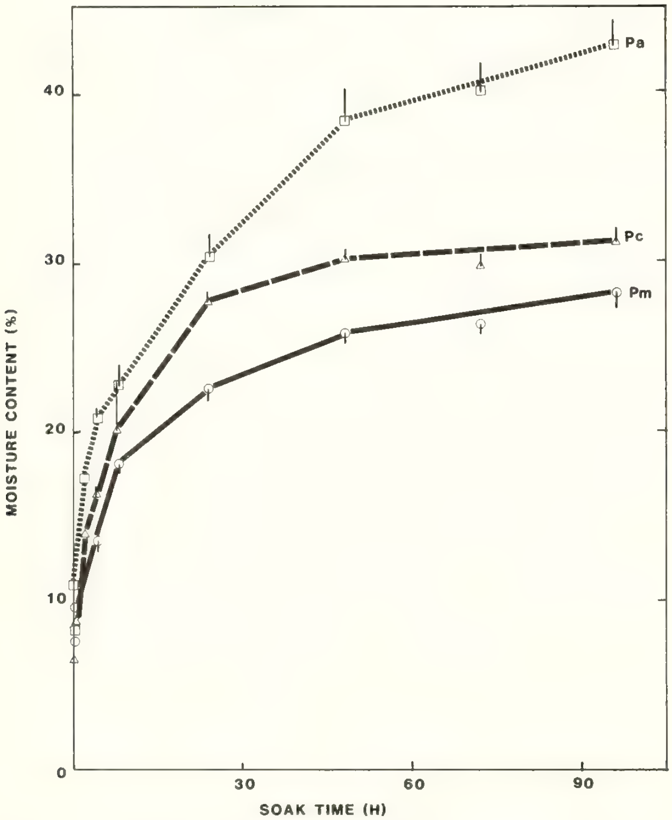


Figure 3.--Moisture content of P. albicaulis, P. contorta, and P. monticola seeds as affected by length of imbibition: □ P. albicaulis, △ P. contorta, ○ P. monticola. Data points are based on the means of 12 separate moisture determinations. Note that only half of the standard error bar is shown for each point.

To assess the degree of dormancy in P. contorta, stratified seeds were compared to unstratified controls. Mean germination of the stratified and unstratified seeds was no significantly different, indicating that physiological dormancy was not present in th lots used in this study.

Generally, it would be expected that germination of clipped seeds by removal of mechanical restraint would be the same or slightly higher than that of intact seeds, b cutting the seeds decreased average germination from 60% to 42% (table 4). Cutting the seeds not only destroyed the integrity of the coats but probably damaged the seeds in other ways, although mold was n a problem in intact seeds, substantial funga growth was present on seeds which had been clipped.

Seedcoats of P. contorta do not appear to mechanically restrict germination, nor do th act as a barrier to water. A study of the water uptake performed on three seed sources showed that seeds were almost completely imbibed within one day (fig. 3). Seeds reached 28% m.c. during the first 24 h and gained only an additional 3% m.c. during the remainder of the 96 h period.

P. monticola

Relative to unclipped controls, clipping the seedcoats increased germination from 10% to 40% (fig. 4). On average, unstratified seed germinated only 8% without clipping, but abo 38% with clipping.

Table 4.--Effects of clipping and stratification on germination of P. contorta

Seedlot	Germination percent		
	+ Strat - Clip	- Strat - Clip	- Strat + Clip
1427	54.3[a]	54.5[a]	45.5[a]
1806	62.0[a]	60.3[a]	36.3[b]
2112	57.8[ab]	68.5[a]	42.5[b]
2238	59.8[a]	57.5[a]	41.5[b]
MEAN	58.5	60.2	41.5

Seeds were soaked for 24 h, stratified for 3 wk at 2°C, and incubated at 30°C/20°C with 8 h light for 3 wk. Means with the same letter are not significantly different at p=0.05.

ıtratification consistently increased ıermination capacity but the degree of 'esponse varied with the treatment and seed ;ource. For lot 633, stratification for 60 'ays at 2°C was most effective, but for lots 49 and 3249, the best treatment was 90 days t 2°C. For stratified and clipped seeds, ermination was 73%, 82%, and 92% for lots 33, 849, and 3249, respectively.

he two alternate stratification techniques ere less effective than the standard method. n the stratification-redry technique treatment 3), moisture is controlled during ıtratification by chilling seeds for 30 days t 40% m.c., then for 90 days at 30% m.c. Danielson and Tanaka 1978). This treatment as proven effective in releasing Abies pecies from dormancy (Edwards 1982; Leadem 985). However, performance of P. monticola as very poor using this treatment, averaging nly about 10% germination (fig. 4). It ppears that the redry method either requires ome modification before being applied to P. nticola, or alternately, is entirely nsuitable for breaking dormancy of these eeds.

Compound stratification was included because it is frequently used for immature seeds to enhance embryo growth, however, when tested on P. monticola, germination was usually not greater than that of unstratified seeds (fig. 4). However, response to a stratification method promoting embryo growth was not expected, because embryos appeared to be fully elongated in X-rays taken prior to treatment.

Although seed coats imposed a significant obstacle to radicle protrusion (fig. 4), they did not constitute an appreciable barrier to water uptake (fig. 3). Water uptake by P. monticola seeds, although less than the other two pines, was virtually complete within 48 h. Moisture contents of intact seeds which averaged 26% at 48 h had only increased to 28% by 96 h.

DISCUSSION

Seed immaturity, as well as physiological dormancy, was responsible for the poor germination of P. albicaulis. Because the species is found at high elevations, the

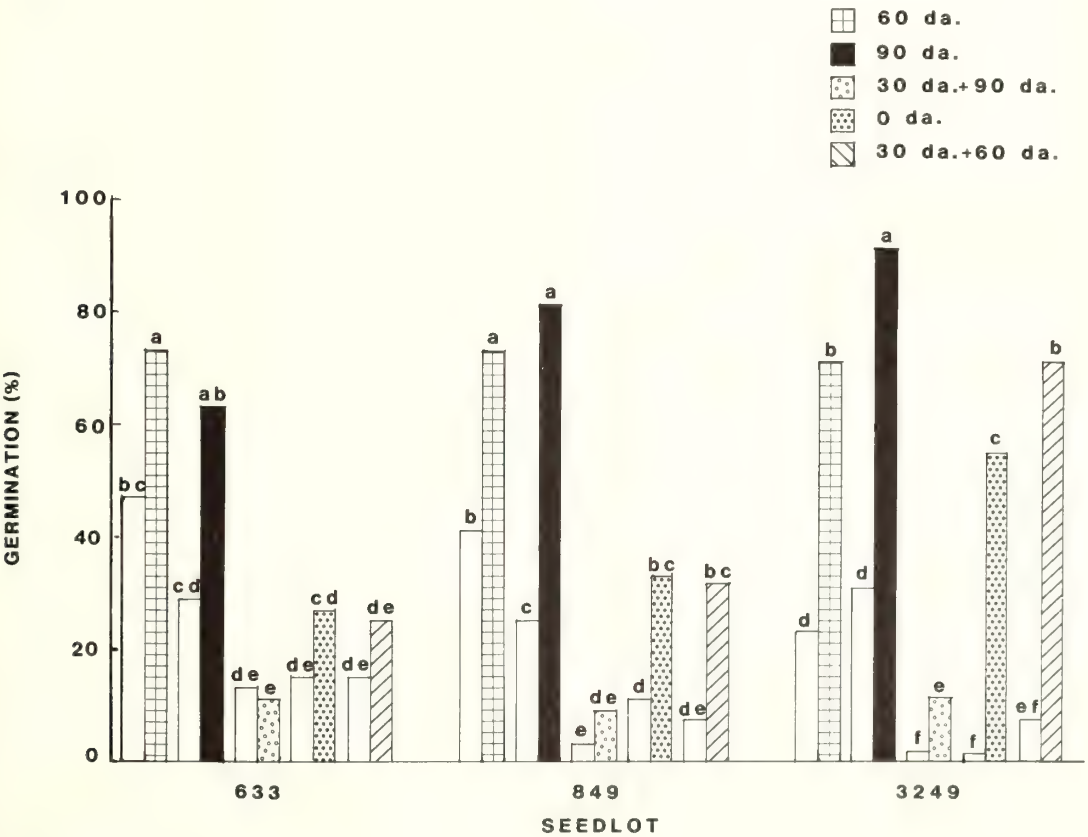


Figure 4.--Effects of clipping and stratification on germination of P. monticola. Stratification treatments are in order as follows: 60 days at 2°C; 90 days at 2°C; 30 days at 40% m.c., followed by 90 days at 30% m.c.; 0 days at 2°C; 30 days at 20°C, followed by 60 days at 2°C. Black and hatched or dotted treatment bars represent germination of clipped seeds, while blank bars are corresponding percentages for intact seeds. Data points are means of six 100-seed replicates. Means with the same letter are not significantly different at p=0.05.

growing season may be limited to a few months, leaving very little time for seeds to mature in the cones. Also contributing to poor development is premature harvesting by the Clark's nutcracker and small rodents such as chipmunks and squirrels. P. albicaulis cones are indehiscent, lacking the tracheid cells which in other pines cause scales to reflex and release the seeds (Lanner 1982). Thus, seed dispersal is dependent upon the dissection of cones by animals foraging for food (Tomback 1981). Unfortunately, foraging animals are not concerned with embryo development and will harvest seeds long before they are mature. As a result, it is often necessary to harvest cones while they are immature to ensure that they are still intact.

The lack of development in P. albicaulis was partially overcome by exposing imbibed seeds to 20°C to enhance embryo elongation, but warm temperatures alone were inadequate to effect dormancy release. Seeds required at least 60 days of cold temperatures (2°C) to overcome physiological barriers to growth. Clipping the seedcoat was also a necessary prerequisite for germination. However, the fact that clipping was necessary indicates that stratification treatments did not fully satisfy the germination requirements of P. albicaulis. Although clipping is considered a measure of mechanical restraint, I feel that mechanical and physiological dormancy are not separate entities. Rather, dormancy should be considered a single phenomenon representing a balance between the mechanical constraint of the coat and the expansive force of the embryo (Chen and Thimann 1966; Barnett 1972). Stratification is an effective dormancy-breaking technique which initiates metabolic processes that may alter the outer seed layers and increase the growth potential of the embryo. It is this increased growth capacity, and to a lesser degree a weakening of outer tissues, which enables the embryo to rupture the seedcoat and germinate. It should be noted that increased growth capacity was not verified in this study because embryo growth tests were not performed. How stratification affects growth potential may be explored in future studies.

The P. contorta lots employed in this study did not exhibit dormancy since unstratified seeds germinated as well, although not as quickly, as stratified seeds. The seedcoat did not prevent radicle emergence, nor did it restrict the entry of water.

For P. monticola, the failure to germinate appeared to be primarily due to physiological dormancy because all three lots used in this study responded best to stratification conducted at 2°C for 60 to 90 days. Two modified stratification techniques were tested in addition to the above methods: combined warm/cold stratification, which is often beneficial for enhancing germination of immature seeds, and the stratification-redry method, which has been shown to be successful when extended stratification periods must be used to overcome dormancy. However, neither of these alternate methods were as effective as the standard stratification treatment at 2°C. A strong component of dormancy seemed to be the restraint imposed by the coat, since clipping the seedcoats increased germination regardless of the type of stratification used. As with the other two pines, seedcoats only affected protrusion of the radicle and did not constitute barriers to water. Thus, as noted earlier, it is not the inability of the seeds to imbibe water which is responsible for lack of germination, but other physiological factors which prevent rupture of the coat.

How can the preceding observations be related to what is known about the habitats and life strategies of the three pines? P. albicaulis is a species which is able to survive in marginal subalpine habitats with short growing seasons. The lack of seed wings and indehiscence of the cones has resulted in dependence on animals for dispersal of the seeds. Seeds frequently do not mature on the tree during the short growing season, but the caching of the seeds in the soil by animals allows the seeds to continue ripening during long storage under the snow. X-ray evidence and results from germination tests reveal large variability in seed development and dormancy. These traits would suit a life strategy whereby only a few individuals germinate at a time so that all regeneration efforts do not occur at once, in the event that conditions are unfavourable. This strategy may be conservative, but is more likely to ensure continuation of the species in a harsh environment.

P. contorta is a pioneer species which is opportunistic in nature. Although it can be found anywhere from dry to wet sites, it is generally a shade intolerant species which starts to decline in importance once the canopy begins to close. As a prominent member of the initial seral stage of ecosystems in which it is found, it must germinate quickly to fill the pioneer niche. Therefore, most seed populations of P. contorta tend not to be dormant. For this species, there would be little advantage to delaying germination since habitats would tend to become less favourable with time.

P. monticola is a widespread species found in mesic environments of the western United States and Canada. Relative to P. albicaulis and P. contorta, P. monticola exists in a stable environment where water, temperature, and shade conditions are generally favourable. There is no necessity for rapid germination, nor must germination be extended over a long period, thus dormancy is probably governed by other factors.

The results of this study indicate that the type of dormancy exhibited by seeds of P. albicaulis, P. contorta and P. monticola can be related to their habitat of origin.

Each species occupies a different ecological niche, and as life strategies vary according to changes in local environments, so would dormancy control mechanisms also be expected to differ. The data show that dormancy does vary between species, although the release mechanisms are presently unknown. The nature of these mechanisms may be difficult to determine because of the variable responses to stratification as shown, for example, by different seed sources of P. contorta (Kamra 1982; Hellum and Wang 1985). Notwithstanding these difficulties, understanding the control of dormancy in coniferous seeds would have significant impacts in both theoretical and applied forestry. Further research in this field is therefore strongly encouraged.

ACKNOWLEDGMENTS

Sincere thanks are given to Sue Baker and Carl White for their expert technical assistance in performing all the experiments reported in this paper.

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NET RETRIEVAL SEED COLLECTION

James L. McConnell and Jerry L. Edwards

BSTRACT: The Net Retrieval Seed Collection ystem is a mechanical seed harvesting system. t has been used successfully in southeastern eed orchards for the past several years. echniques, machinery, and costs for the system re described.

NTRODUCTION

here are well over 6,000 acres (2 428 ha) of oblolly (Pinus taeda), 600 acres (243 ha) of hortleaf (P. echinata) and 300 acres (121 ha) of irginia pine in the Southeastern United States. hese species are all commercially important, ith the loblolly pine far and away the most mportant. Also the seed is considered to be ard to collect because the cone is not easily reed from the limb. Traditionally, collecting ones has been the primary means of collecting eed.

ith such large areas of seed orchards to ollect during the short period between cone ipening and seed fall, seed orchard managers ave sought a better method of collecting the igh-value pine seed needed to reforest the outhern pine wood basket.

ne netting-seed collection concept, which riginated with the Georgia Forestry Commission, nows promise as a method to collect seed. The ommission spread net material over the seed rchard floor and waited for the cones to ripen nd the seed to fall. A hand labor force was sed to windrow the material that had accumulated n the net. The windrowed material was hand-fed nrough a peanut harvester. The peanut harvester id a good job of separating the seed from the ine straw and other trash. Six years ago the SDA Forest Service's Southern Region and issoula Equipment Development Center began evelopment of a system that would mechanize the oncept developed by the Georgia Forestry ommission. The initial goals were to provide system that could be operated by five to seven eople, harvest the seed in a relatively short eriod of time, and do all this in a safe manner.

The initial goals have been met. One net retrieval machine can safely harvest seed from 40-60 acres (16-24 ha), using only five to six persons and do the entire job. Elimination of the need for tree climbing creates a safer, more productive, and less labor-intensive method of seed collection (fig. 1). Except for poor seed years, the system has proven to be cost-effective. The seed orchard managers are extremely pleased. The system is presently on-line at three Southern Region orchards with the fourth scheduled this year. Several State and industrial orchard have begun the use of parts of the system.

Figure 1.--Netting retrieval and seed separation equipment.

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iper presented at the Conifer Tree Seed In The iland Mountain West Symposium, Missoula, MT, igust 5-6, 1985.

imes L. McConnell, Regional Geneticist, Jerry Edwards, Mechanical Engineer, USDA Forest ervice, Southern Region.

the net used in the system is a polypropylene plastic fabric manufactured initially as a backing for carpets. Knitted monofilament polyethylene fabric designed as shadecloth has also been used successfully (fig. 2).

Figure 2.--Net (polypropylene plastic).

Optimum seed fall in the South usually occurs in November, but as with most outdoor activities, it depends on the weather. As weather fronts move through, rain occurs; after the front passes, several cool, dry, sunny days occur bringing good collecting conditions. The netting is spread over the orchard floor several weeks before cone opening (fig. 3).

Figure 3.--Orchard floor covered with netting.

As the cones open, orchard trees are shaken with mechanical tree shakers similar to those used to shake pecan trees. The specially designed cushioned clamping pads, when attached to the tree, tend to protect the tree and, at the same time, transmit the shaking energy to the tree. The omni-direction shaking characteristics developed by the shaker head removed nearly all the seed from the open cones. Experience has taught us that minimizing tree damage depends on a competent, well-trained tree shaker operator. A second shaking prior to retrieval yields additional seed from the cones. When the seeds have been dislodged from the cones and have fallen into the net, one end of the net is attached to aluminum pipe core which has been secured to the net retrieval machine. The retrieval machine operates by turning the core and rolling the net onto the core. Seed, pine straw, and other debris on the netting is dumped onto the retriever conveyor as the net i recovered and fed into the seed separator. The seed separator separates the seed from unwanted material (pinestraw, cones, sticks, etc.). The large amount of relatively clean pine straw processed can be bailed and used as mulch in nurseries or sold for landscaping.

The seed, as it comes out of the seed separator is only roughly cleaned and requires additional cleaning and processing before being placed in cold storage. The seed receives additional processing at a conventional seed extraction facility. The seed requires fine cleaning and introduced into the conventional processing equipment just after the cone tumbler and goes through the remainder of the seed cleaning/processing equipment. There is a substantial savings in cost since the expensive cone drying-opening process is eliminated.

EQUIPMENT

Power requirements to operate the netting retrieval and seed separation equipment are les than 30 PTO horsepower (34.4 kilowatts). The PTO power is used to drive a hydraulic pump tha supplies the power to operate the machinery.

An operator's station is located at the rear of the retrieval equipment. From this location, a machine functions can be observed and controlle

COLLECTION COSTS

In 1983, the net collection process produced 1,649 lb (748 kg) of loblolly pine seeds from 141 acres (57 ha) at three Southern Region seed orchards. Overall, 1983 was not a good se collection year; total production and yield wer down. The seeds were collected at the followin orchards: Francis Marion, South Carolina; Erambert, Mississippi; and Stuart, Louisiana,

Variable Costs.--Labor and general-type equipme (vehicles, wheel tractors, etc.) costs totaled $29,920.

Fixed Annual Costs.--Fixed costs for 1983 were:

Item	Total cost	Expected life	Annual amortization
Netting	$316,214	10 years	$31,621
Cores	14,040	20 years	702
Retrieval Equipment	144,480	20 years	7,224
		Total	$39,547

Cost of net collection, 1983.--Total costs of ne collection for the year were:

Category	Total Cost	$/acre	$/ha
Variable cost	$29,920	$212[1]	524
Fixed cost	39,547	280	692
Total	$69,467	$492	$1216

[1] Number of acres = 141 (57 ha)

983 COLLECTION

:ones collected in 1983 from the same orchards ·ielded 1.14 pounds of seeds per bushel (0.12 :g/dl). The seeds collected from the netting ;ystem weighed 1,649 lb (748 kg). The equivalent ıumber of bushels of cones required to yield the ;eeds obtained from the netting is 1,446 bushels 5 096 dl). The collection of cones obtained ›y contract or force account (using Forest ;ervice workers) would have been $33 per bushel $9.35 per dl):

Collection	$30
Drying and extraction	2
Transportation to extractory	1
	$33/bushel
($9.35/dl)	

'he cost of cone collection FY 1983 (hypothetical) ıs $47,718 (volume of seed X cost/unit).

he comparison of costs (cone collection versus etting system) was:

$69,467	Cost of net collection
-47,718	Cost of cone collection
$21,749	

his proves that cone collection would have been ore economical.

984 COLLECTION

n Fiscal Year 1984, 4,529 lb (2 054 kg) of oblolly pine seeds were collected from 216 cres (87 ha) within the netting systems from he three Forest Service seed orchards mentioned arlier. Seed production was spotty; east coast ollections were light, but Gulf coast collections ere good to heavy.

ost of net collection in 1984 was:

Category	Total cost	$/acre	($/ha)
ariable cost	$48,575	$225[1]	$ 558
ixed costs	39,547	183	454
Total	$88,122	$408	$1012

No. of acres = 216

he cost of cone collection in 1984 (hypothetical) as $104,511 (volume of seed X cost/unit).

he comparison of cost (cone collection versus etting system) was:

$104,511	cost of cone collection
- 88,122	cost of net collection
$ 16,389	

ıis proves that net collection would have been ɔre economical.

ESULTS AND DISCUSSION

ıe cost of the net seed collection system is reatly affected by the volume of seed vailable. The larger the volume of seed on the net, the lower the cost per pound (kg) of the seed. Retrieval and quality of separation of the seed is virtually unaffected by the volume of seed. On the other hand, the volume of debris (pine straw, twigs, etc.) on the net has a measurable effect on the rate of separation.

In general, the smaller the seed and cone crop, the more the advantages are in favor of cone collections. When the crop is small, the cones can be selectively collected; however, it is nearly impossible to selectively deploy netting and still catch the seed fall.

The equipment now used for the net retrieval system is considered a first-generation production prototype. Many improvements will be made to produce a more efficient and compact system. The cost of equipment may continue to rise, but probably not as fast as the cost of labor, especially the trained labor force that is required in cone collection.

The initial costs of the net retrieval system are high. Therefore this system would not be economical in young orchards or an orchard with a low production capacity. The following factors can be used to decide whether to use the net system or harvest cones in a particular year:

Net Seed Collection System

1. Number of acres (ha) of orchard under consideration.
2. Calculated production capacity of the orchard (number of bushels (dl) of cones or pounds (kg) of seed in the orchard under consideration); end product will be pounds (kg) of collectible seeds.
3. Cost of deploying and recovering the net seed collection system on the following basis: a five-person crew operates at the rate of 0.25 acres (0.11 ha) per crew per day. This work includes the total job of deploying the net, shaking the trees (twice), retrieving the net, processing the seed, and returning the rolls of net to storage. The time sequence becomes relatively unimportant, because much of the job takes place before and after the cone ripening period. With this information, the orchard manager can calculate the price of seeds per pound.

Cone Collection System

1. Price per bushel (dl) to collect cones, transport them and extract the processed seed.
2. Can the cone crop be picked before cones mature to the point of opening?
3. Is an adequate supply of collection equipment available?
4. Is there an adequate pool of people to do the work safely?

If the price per bushel (dl) for the netting system is higher than that for harvesting cones, the orchard manager would then decide that, in all probability, cone picking will be the most economical method.

Every orchard and organization will generate a different number, but we feel the net retrieval seed collection system is a viable alternative to a difficult job. Netting material and tubing specifications are shown in the appendix.

APPENDIX

Netting material specifications

Material: Polypropylene/polyethylene plastic
Width: 16 ft, 5 inches (4.75 m)
Length: 350 ft (106.16 m)[1]

Salient characteristics:

Color	- Black
Weave count	- 6 X 8 per in^2
Weight	- Minimum 2.1 oz per yd^2 (50 g per m^2) Maximum 3.0 oz per yd^2 (17.4 g per m^2)
Tensile strength	- Minimum 60 lb warp (27 kg) warp (length) Minimum 70 lb (31.5 kg) fill (width)
Burst strength	- Minimum 175 lb per in^2 (12.2 kg per cm^2)
Yarn stability	- Minimum 1 oz (250 g)
Cores	- All cores to be continuous in lengths 17.25 ft (5.23 m) overall
Outdoors wearing	- Minimum of 70 percent retention after 400 hr in weather-o-meter.
Selvedge edge	- Minimum of 0.25 inch (0.64 cm) selvedge area for each edge.
Cost	- \$1.62/lineal yd (\$1.47/lineal m) @16'5" (4.75 m) width \$1418/acre (\$3545/ha) --1982 contract price

Source of supply:

Amoco Fabrics Company
Patchogue Plymouth Division
550 Interstate North Parkway
Atlanta, GA 30339
(404) 995-0935

Weathashade
568 West Orange Blossom Tr.
Apopka, FL 32703
(305) 889-3692

[1]Length can be varied to meet needs of the individual orchard.

Core (tubing)

Material:	Aluminum Alloy 6063 T6
Diameter:	4.0 inches (10.6 cm) outside diameter
Length:	17 feet, 3 inches (5.23 m)
Weight:	0.73 lb per lineal foot (56.5 g per lineal m)
Specification:	Federal Specification QQ-A-200/9c
Cost:	\$20/piece (approximate) --1982 contract price

Source of supply:

Reynolds Metals
6601 Broad Street
Richmond, VA 23261
USA (804) 281-2655

DOUGLAS-FIR SEED COLLECTION AND HANDLING

Richard M. Schaefer III and Daniel L. Miller

STRACT: High-quality conifer seed is a must for cessful and economical seedling production, ecially in containerized operations. High-ality seed is characterized by high percent mination (90+), uniform germination and insig-icant mold and disease problems. High-quality d can be assured by attention to details during lection, handling, and processing. Collections uld be made only after the seed has fully ured. Immature collections result in reduced erratic seed germination. Proper cone handling storage methods will prevent problems associa- with cone heating and molding. Skillful cessing will produce clean, dry seed and will serve the germination potential obtained ough proper collection and handling.

RODUCTION

d collections must stress quality as well as ntity. Seed quality is especially important in enhouse nurseries. As containerized seedling duction increases so does the need for high-lity seed. For instance, using a seed cost of 00/M seedlings, increasing germination from 50 to percent increases seed value by five times ble 1). Actual growing costs associated with the er germination potential seed are considerably her than the single-sown 95+ percent germination d because the increased seed volume means higher atification, sowing, and crop thinning costs. itional savings for 95+ percent seed could be as as $5-$10/M in container nurseries. The 95+ cent germination seed also reduces grower risk n additional failures caused by fungus and low-r seedlings resulting from poor quality seed.

le 1.--Douglas-fir seed values per pound for a containerized nursery assuming a $5.00/M seedling seed cost

ination ercent	Seeds per Cavity[1]	Seeds Per Pound 25M	35M	45M
95+	1	$125	175	225
75	3	42	58	75
50	5	25	35	45

sumes a sowing rate that will produce at least percent stocked containers.

er presented at the Conifer Tree Seed in the nd Mountain West Symposium, Missoula, MT, ust 5-6, 1985.

ard M. Schaefer III is Seedling Production ervisor, and Daniel L. Miller is District ester, Potlatch Corporation, Lewiston, ID.

High-quality seed also reduces seed inventory and storage costs. Prior to implementing the procedures described here, our Douglas-fir seed germination rates ranged from 12 to 39 percent. Assuming this seed is usable in our nursery, we would need an additional $675,000 in seed inventory to operate at current capacity. High-quality seed is also important in bare root nurseries, especially as precision seeders come into use.

These dollar values become more important when you consider that obtaining high-germination seed costs no more than obtaining low-germination seed. The secret to high-quality seed is attention to detail. Cones must be harvested when seed is ripe and handled and stored so as to preserve seed quality. It costs just as much to harvest immature seed with 30 percent germination as it does to collect mature seed with 90 to 100 percent germination. In fact, immature or insect damaged seed is often more difficult to extract. This increases processing costs and reduces seed yields.

The methods described here were developed from communications with the late Mr. Charles Brown of Brown Seed Company, Vancouver, Washington. Charlie's methods were developed during more than 30 years of working with conifer seed. His goal was to produce the best possible conifer seed. To do this, he found that the cones must be fully ripe when collected and stored under proper conditions. If not, seed viability was reduced. His cone maturity indicators are the result of years spent observing cone ripening. These cone handling procedures were developed to prevent molding which reduces seed germination and avoid cone heating which causes varying dormancy levels. Under Charlie Brown's direction, Brown seed earned the worldwide reputation of being the best available. This is ample testimony that his procedures work.

The following are Brown's methods that Potlatch foresters are using. These methods have resulted in the collection of consistently high-quality Douglas-fir seed with germination rates of 85 to 99 percent.

SEED INVENTORY PLANNING

Douglas-fir usually produces a medium to heavy cone crop once every five to seven years in northern Idaho. At Potlatch, we strive to maintain a five-year seed supply on hand for each seed zone. We have delineated seed transfer zones by ± 500-foot elevation classes and by 15-mile geographic distance within the same habitat type. Five-year harvest plans are used to estimate the number of seedlings and amount of seed needed for each zone. Collections are scheduled only during heavy cone crop years

unless seed inventory is low for specific zones. Estimated seedling needs are converted to pounds of seed and bushels of cones for planning and budgeting purposes. These estimates are developed during the winter so that selected areas can be checked for potential cone crops in early spring. This planning also allows scheduling logging to prevent harvest in selected collection areas prior to cone ripening. This is especially necessary for fall-and-pick cone collections, our preferred method. Also, other stands may be reserved as permanent cone collection areas. This is especially important if there are few trees of the desired species of cone bearing age within the seed zone.

EARLY CROP ANALYSIS

Potential cone crops can be evaluated as early as mid-June. By then, the female cones have been pollinated and are large enough to be easily seen. Also, cones damaged by spring frosts can be easily identified. These turn red-brown and shrivel. Cone crops can be rated as follows:

Light crop - few scattered cones, usually near tree top and limb ends.

Medium crop - several cones per limb, majority in the upper 1/3 of crown.

Heavy crop - 10-20 cones per limb and extending down most of the crown.

For a crop to be rated heavy, most of the trees in the stand should have heavy crops. Scattered trees with heavy cone crops don't necessarily indicate a good collection year. Unless seed is badly needed, collections should not be scheduled in light to medium crop years. Seed yield is generally poor in light to medium crop years because of poor pollination and increased insect damage. Seed and cone insects may destroy nearly all seed during light crop years. Since it costs as much to collect wormy cones as good ones, collections should be scheduled when you can get the most seed for your efforts. An elementary but important fact to remember is that collection costs and extraction costs are rather fixed; the amount and quality of seed recovered is the major variable. So unless seed inventories are critically low, only moderate to heavy crops should be collected to avoid higher costs and lower percent germination lots.

Seed count monitoring should begin in mid-July. By then, seeds have developed far enough to produce accurate counts. Cones may be picked or shot down for inspection. Check cones for insect activity. Mid (July) season insect attack shows as curled, brown tipped or dead, dry cones. Insect bore holes and frass may also be evident. Insect damage may not be easily noticed, however, so cut tests should be a standard part of crop evaluation procedures. The cut test is made by slicing cones longitudinally down the center with a sharp knife, hatchet or cone cutter.

Tests are conducted as follows:

- Sample at least 10 cones from each of 4 to 5 trees selected at random in the stand.
- Count all sound filled seed on one face of the cut cone. Filled seed have white centers (endosperms). Aborted seed are darkened or shriveled. Look for insect activity inside the seed.
- If more than half of the cones sampled have insect damage, subtract one sound cut seed from the count on each damaged cone. Insect-damaged cones often do not fully open during processing, preventing extraction of all sound seed. Adjusting the seed count compensates for this.
- The number of filled seeds should average at least 5 for economic harvest. Lower counts can be accepted depending on the need for the particular source.
- A 6 or better count is considered adequate for a large collection effort.

Samples should be collected on at least two-week intervals to monitor maturity and insect damage. Insect damage will increase as the summer progresses. Some crops that appear good in July may be completely destroyed by harvest time.

COLLECTION PLANNING AND PREPARATION

Planning cone collection activities involves determining the type of collection. Preparation involves obtaining needed equipment and preparing storage facilities. The type of cone collection -- climb and pick, fall trees and pick, or squirrel cache -- will have an effect on seed quality. Unless absolutely necessary, squirrel cache collections are avoided because it is impossible to consistently get 90+ percent germination from squirrel-cut cones. This is due to two factors:

1. Squirrel cache collections are characterized by inconsistent maturity levels and large variations in dormancy, resulting in lower and extended germination. The squirrels do not always wait until seeds are fully mature before cutting cones.

2. Squirrel cache collections have the high probability that cones and resulting seed will be highly contaminated with various disease-causing fungi. This is due to the cool, moist environment in the cache. Tests run at the Potlatch greenhouse facility have shown up to 14 times more germinate mortality in Douglas-fir squirrel cache seed lots than in hand-picked seed lots.

In many of the squirrel cache lots, correlation between germination tests and greenhouse performance is very poor. Hand-picked cones, on the other hand, usually have operational performance similar to that of current germination tests.

eparation is one of the most important steps llowing confirmation of the collectible cone crop. is involves:

1. Having adequate field personnel to handle cone maturity checks and clean, bushel, and tag cones.

2. Providing a secure area adequate for daily cone storage.

3. Having enough clean 1.5-2 bushel burlap collection bags. Dirty or previously used bags may reduce quality enough to lower the percentage of the germination testing.

4. Determining numbers, volumes, and species to be collected in each area.

5. Giving proper notification to the required number of cone pickers to handle the harvest. This would include the type of harvest, prices paid to collect, cut test specifications, acceptable maturity, etc.

6. Obtaining adequate field storage racks and developing cone transportation plans. Long-term storage requires a covered area to protect cones from rain and rodents that allows adequate air flow for drying.

NE MATURITY MONITORING

ne maturity monitoring is a prerequisite for heduling collections. Maximum seed germination possible only when cones are harvested when the ed is fully ripe. Early harvests reduce germin-ion. Immature seed are more difficult to extract, ve lower germination and highly variable dormancy d may lose viability in storage sooner than mature d. If in doubt, wait. It is wiser to lose some d due to cone opening than to waste time and lars processing immature seed. Cone and seed racteristics provide our most reliable maturity icators. Year-to-year fluctuations in weather terns affect cone ripening and make it impossible set calendar dates for harvest. Elevation also ects maturity dates. Therefore, on-site cone pections at each collection point provide the t reliable information for scheduling cone har-t. Remember, a sound regeneration system is ed on mature, high-quality seed.

es should be checked at least every two weeks ing July and early August. These checks will ntify insect losses. Weekly or twice weekly cks should be made as cones mature. Cone color not the best indicator of seed maturity. Examine seed. Often it will mature before cone color nges. Mature seed endosperm is quite firm, nut-e and not milky or runny. Squirrel activity uld not be used as a basis for starting collection ivities. Squirrels are interested in food, not percent germination seed. A good example of the irrel's inability to evaluate seed maturity urred in 1980. Several seed companies collected es grandis cones in north Idaho from squirrel ne sources. The seed extracted from several dred bushels had such low germination percentages that the seed was not marketable. This could have easily been avoided by people trained to personally evaluate cone maturity.

The following Douglas-fir seed and cone maturity descriptions were developed by Charlie Brown and have been used successfully by Potlatch foresters since 1977.

Seed

Immature seed are white to cream-colored with clear to white wings. As the seed matures, the seed coat turns tan then dark tan as the wing turns brown. Mature seed has a golden brown seed coat with completely brown wing.

Cones

Immature cones are green. As they ripen, they acquire a yellow tinge like a ripening banana--not bright yellow but slightly yellowish. As they lose their yellow tinge and begin turning brown, they puff up. Bracts turn brown first and are the first indicator of approaching maturity.

Seed is ripe when cones puff. This is weather related. High humidity will keep ripe cones tight. Cones won't drop seed until they turn brown and open.

Cutting mature cones logitudinally through the center will reveal brown lines (seed wings) running from the seed to the scale tip. If the brown wing isn't obvious, the cone isn't mature. The cut surface of immature cones will turn brown (like a cut green apple) within five minutes. Near ripe cones will too, but not as rapidly.

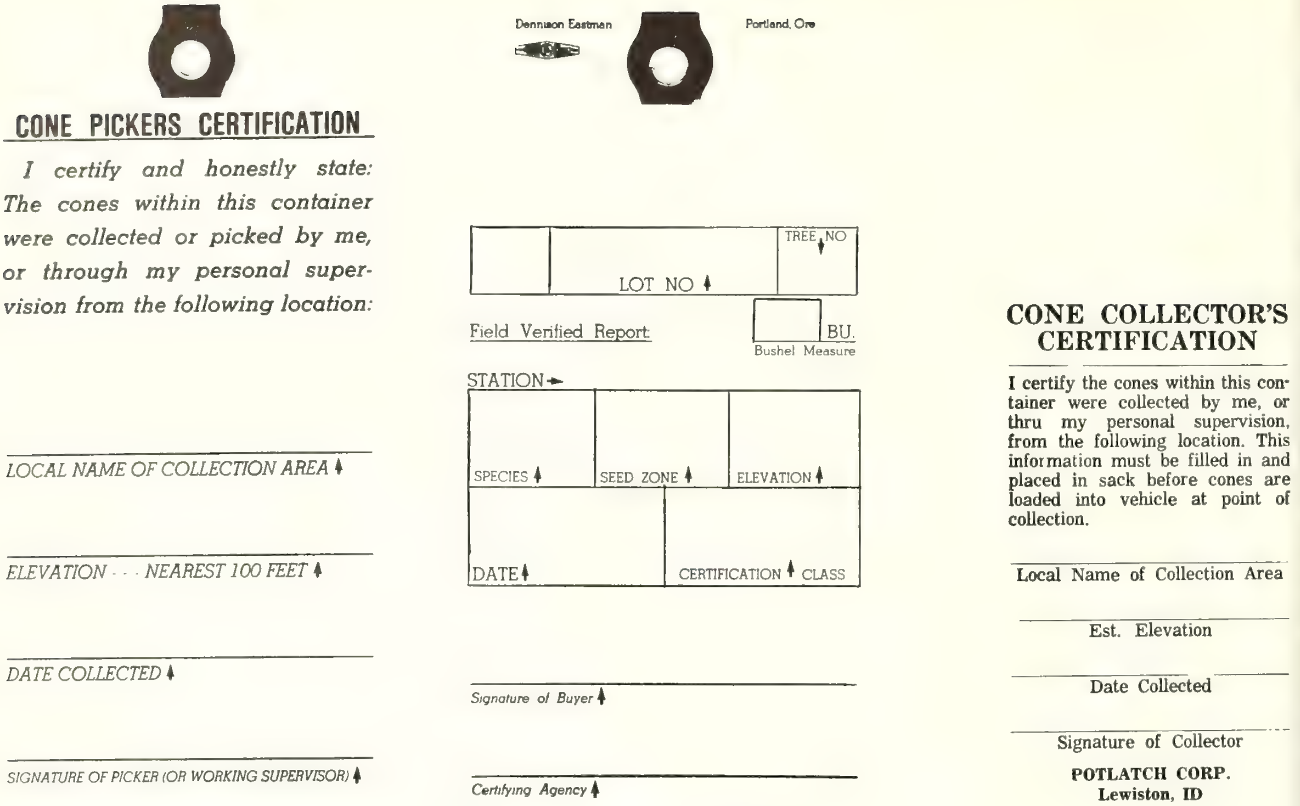
CONE HANDLING AND STORAGE

The following guidelines will ensure quality seed from the cone receiving station to the processor:

1. Cone pickers are required to turn in harvested cones daily. Filled sacks should be kept in the shade during the day and not stacked together, especially not in car trunks. Cone heating must be prevented.

2. All cones are run over a cleaning table to remove debris, check maturity, perform cut test counts, measure for payment, and label. Bags are double tagged--one inside the bag and one tied on the closure (figure 1).

3. A maximum of one bushel of cleaned cones is placed into 1.5-2 bushel sized loose-knit burlap bags. This allows room for air circulation as cones expand and open. The bag is placed as quickly as possible on a portable field drying rack. Quite often, short distance transport of cones to a more central area is required. Since fresh-picked cones are quite susceptible to heating, arrangements must be made to have the green cones shipped immediately, unloaded, and re-racked before heating damage occurs. Green cones will heat, just like piles of wet hay or


CONE PICKERS CERTIFICATION

I certify and honestly state: The cones within this container were collected or picked by me, or through my personal supervision from the following location:

LOCAL NAME OF COLLECTION AREA

ELEVATION - - - NEAREST 100 FEET

DATE COLLECTED

SIGNATURE OF PICKER (OR WORKING SUPERVISOR)

Dennison Eastman   Portland, Ore

LOT NO   TREE NO

Field Verified Report   BU.
Bushel Measure

STATION

SPECIES   SEED ZONE   ELEVATION

DATE   CERTIFICATION CLASS

Signature of Buyer

Certifying Agency

CONE COLLECTOR'S CERTIFICATION

I certify the cones within this container were collected by me, or thru my personal supervision, from the following location. This information must be filled in and placed in sack before cones are loaded into vehicle at point of collection.

Local Name of Collection Area

Est. Elevation

Date Collected

Signature of Collector

POTLATCH CORP.
Lewiston, ID

Figure 1.--Cone bag tags used successfully in Potlatch operations.

grass. Green cones can be stacked together for 1-4 hours; you can test for heating by putting your hands between the piled sacks. Cone heating can reduce dormancy homogeneity that affects stratification time and produces mold problems.

4. To promote seed lot homogeneity, the fresh field-racked cones should be allowed to "after-ripen." This simply means the cones should be kept for approximately a two-week period in a dry, shady, well-ventilated, cool area. This allows the cones to slowly begin drying. During this period, the seeds in each cone have time to reach almost equal dormancy levels; if done properly, this can apply to the entire seed lot. After proper stratification, the result will be quick, uniform seed germination.

5. Following after-ripening, cones may be air-dried before shipment to the processor. If early shipment for long distances is required, precautions are needed to avoid cone heating. Potlatch Corporation has found, in our northern Idaho climate, that two months of air drying brings the seed moisture levels down to approximately 15-20 percent. At this level, there is no trouble with cone heating if the bags are tightly stacked for 24 hours. Each person responsible for collections will have to determine how best to avoid cone heating.

The final link in the process of obtaining high-quality seed is the extracting and processing facility. Improper cone and seed processing ca negate all the care taken in the collection pro Only processors with a good reputation for prod clean, high-quality seed should be used. If possible, visit the facility and observe their procedures. High-quality seed is clean. It do not contain pitch nodules or other inert debris. It also does not contain damaged seed. Blank s should be removed during cleaning and proper processing will not produce cracked or damaged seed. Properly handled and processed seed shou smell good, not sour.

TEAMWORK NEEDED

To produce high-quality seed, all steps from inventory planning through collection and cone storage must be done correctly. Improper metho applied anywhere in the process can substantial reduce both seed yield and germination. Since vigorous, high-quality seed is necessary to pro seedlings that meet rigid specifications, both field personnel responsible for seed procuremen and nursery managers must work together to assu that proper seed collection procedures are adhe to.

AERIAL CONE HARVESTING IN BRITISH COLUMBIA

D.P. Wallinger

STRACT: Early attempts to devise an efficient ans of harvesting cones with the use of a licopter were not totally successful but the sults were promising enough to encourage ntinuing development. At present, two thods--raking and clipping--meet air ansport and safety guidelines, and are in mmon use.

raking, a basket-like device is lowered over e upper tree crown and the cone-bearing anches are stripped from the stem as the unit raised by the vertical lift of the licopter. In clipping, the helicopter hovers the upper tree crown while an operator, ing a hydraulic pruner or electric chainsaw, ts and recovers the cone-bearing top or anches.

ch of the methods has specific applications d limitations regarding stand type, species, d weather. Operating procedures and training quirements for clipping have been identified d documented. Productivity of aerial cone rvesting has been shown to be competitive th traditional collection methods and a gnificant volume of cones is now collected ially in British Columbia.

CKGROUND

harvesting of cones by aerial means had bably been on quite a few minds for quite a years, but it wasn't until the mid-1970's at somebody did something about it.

first knowledge of an aerial system was the on collecting device conceived by Pete issen of Pacific Northwest Region, U.S. est Service, in 1974. This system has come be known as aerial clipping and will be cussed in more detail later. It is also the ndard method of scion collecting in British umbia today.

1974, Okanagan Helicopters, with Forest vice input, fabricated a suspended, unmanned device for collecting scion material. However,the "Cage" suffered from cold weather stress and was scrapped.

In 1976, two forest companies adapted the clipping system for operational collection of Abies amabilis fir. In one case, the cone-bearing branches were clipped and stowed in the poly-lined passenger compartment. On the other project, an operator hooked a small choker on the stem and cut off the top with a small chainsaw. The recovered top was suspended from the cargo hook as other trees were harvested.

Concurrent with these developments, Jack Walters at the University of British Columbia Research Forest had designed an aerial cone rake. Jack's unit was developed under a service contract with the Canadian Forestry Service and was operationally tested in fall 1976. True to Jack's philosophy of "think big," the rake was enormous. It stood 7 m (23 ft) high, was 4.5 m (15 ft) in diameter at the base, and weighed over 800 kg (1800 lb). While the unit's performance was not favorable on a cost-benefit basis, Jack's creation provided the spark that was needed to get things "off the ground."

In the next year or two, the sky was filled with all kinds of raking hardware--kind of like a forestry space program. Most of this metal joined the "Cage" on the scrap heap. Two commercial developers did design successful rakes, but only one has survived.

In the meantime, aerial clipping on a production scale was becoming reasonably successful. Equipment was more sophisticated and procedures refined. An electric chainsaw was introduced as an option to the hydraulic pruner.

The "flying gondola" was conceived aft r a monsoon bucket had been used for sampling during the spruce budworm outbreak of 1975-1976. First thought of as a means of scion collecting, the gondola quickly became a vehicle for cone harvesting. The bucket was slung beneath a Long Ranger and maneuvered into the treetop. The saw operator, riding in the bucket, set a small choker around the stem and sawed off the top. The severed top hung from the bucket while subsequent trees were harvested. This was a highly productive system

er presented at the Conifer Tree Seed in the and Mountain West Symposium, Missoula, MT, ust 5-6, 1985.

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and two or three units were built and used in 1979. Unfortunately, because a single-engined helicopter was used, the method was grounded by the Federal Ministry of Transport. Its use would likely be permitted if two-engined aircraft were used but the economics of the method would be unfavorable.

So that leaves us, at present, with two approved aerial harvesting systems--raking and clipping.

RAKING

The term "rake" loosely refers to branch collectors, strippers, or cutters. The configuration is generally a circular or hexagonal fiberglass cone at the top of which is a large opening with wide, radiating slots, each of which is bordered by upward-oriented cutting edges. Around the circumference of the base is a vertical fence of expanded aluminum welded to a frame. The diameter of the rake is normally about 2 m (6.6 ft). From three points around the circumference of the upper frame, light cables rise to a common ring to which the helicopter's cargo hook is attached. The unit may weigh between 130 and 150 kg (285-330 lb).

In practice, the rake is centered over the target tree and lowered until most of the cone-bearing branches protrude through the upper opening of the rake. The helicopter then lifts the rake and the cutting edges sever the limbs which are then retained by the surrounding mesh. Two or more lowering and lifting sequences may be required to harvest the majority of available cones from a tree. Harvesting takes about 30 seconds per tree. The pilot then proceeds to other trees and repeats the procedure until he has a safe maximum payload.

At the landing, while the helicopter hovers, the dumping mechanism is activated by the ground crew and the collected material falls free of the mesh enclosure. Any pieces hung up in the rake teeth are cleared by hand. The dumping device is then secured and the machine leaves for another cycle. A cycle is defined by a series of harvesting events--lift-off, fly-out, harvest, fly-in and unload. Cycles are usually under 15 minutes during which time eight to twelve trees may be harvested. Pilot fatigue is a safety consideration and two pilots usually alternate the flying task every hour or so. A day's collecting lasts about 7 1/2 hours or 3 1/2 hours per pilot.

The Bell 206L-1 (Long Ranger) or Hughes 500 are adequate machines for raking. In 1979, it was determined that, to be successful, aerial rakes must be:

a) simple in design and easily maintained;
b) light in weight but strong;
c) suitable for several species and capable of harvesting several trees in one flight;
d) stable in flight and easily maneuve[rable]; and
e) efficiently unloaded.

The rakes in use today meet these criteria [a]nd they are very efficient for harvesting the species for which we have a large demand, namely true firs, spruces, and Douglas-fir.

Rakes can be used in all types of terrain. They can be ferried short distances between collection areas or can be transported over longer distances by pickup truck. New unloading mechanisms enable harvested mater[ial] to be dumped into the box of a large truck [an]d hauled to a central picking facility.

With improvements in rake design and experience, productivity has become quite favorable. In fact, collecting true firs b[y] conventional methods could never match the productivity of the rake.

The only drawback to raking is that the selection of phenotypes is left up to the pilot. In our situation, where considerabl[e] emphasis is placed on collecting only from better phenotypes, we are dependent on carrier-employed pilots. They are usually anxious to maximize productivity, and we al[l] know that the most cones are not always on [th]e best trees.

Another concern with raking is cone recover[y]. Our best estimate is that only about 50 per[cent] of the cones on a tree are recovered. As l[ong] as there are lots of trees available, this [is] not a problem, but when a quota must be tak[en] from a stand with a limited number of cone-bearers, cone recovery is important.

CLIPPING

The development of clipping to its present state has been a cooperative effort between [the] Ministry of Forests and the carriers who ha[ve] done the flying for us.

The system involves some modifications to t[he] aircraft itself. It must have:

a) low skid gear - no bear paws;
b) front and rear doors on the right si[de] removed;
c) live-mike capability between pilot a[nd] clipper operator;
d) a barrier between the rear and forwa[rd] cabin areas;
e) the rear cabin lined with poly;
f) an E.L.T. (Electronic Locator Transmitter);
g) a hanger for the clipper installed b[y] the right hand step; and
h) a counter-balancing weight secured i[n] the left side of the forward cabin t[o] maintain center of gravity.

Following several incidents in 1982, the Ministry of Forests set up a committee to review the aerial clipping system and to establish operating procedures. In coopera[tion]

ith the air carriers, an operations manual and formal training program were produced by the inistry and are now in place. Because clipping emands precise flying, pilot requirements and ualifications are stringent. Clipper perators must undergo an intensive "hands-on" raining course. The pilot and operator must ork as a team, so their personalities must be ompatible.

riefly, the clipping unit has three omponents. The auxiliary power unit consists f a battery pack and is independent of the elicopter's electrical system. However, the attery pack can be replaced by connecting the ydraulic pump unit directly into ship's power.

he hydraulic pump consists of an electrically riven hydraulic unit, a hydraulic reservoir, nd switching valves. The electrical circuit an be activated by a master switch.

he third component consists of the ydraulically operated clipper head, hydraulic oses, and an electrical cable which leads to n operating switch on the handle of the lipper. The clipper must cut through a 6-cm 2 1/2-inch) stem in three seconds.

ne electric chainsaw option is made up of two omponents. A generator is mounted to the left ront floor of the aircraft and is wired to the ircraft's electrical system and produces 10 volts to power the chainsaw. The electric hainsaw is equipped with a short bar and a pecial guard which covers the entire chain xcept for a 6-cm (2 1/2-inch) opening along ne underside of the guidebar.The operator ears natural-fiber coveralls, appropriate ootwear, suitable gloves, and a secured and isored helmet fitted with voice-operated eadset. In the clipping position, the perator is seated on the step of the right ear door with his feet on the skid. He is ecured to the aircraft by a special body arness attached to an interior hard point and lso by the regular seat belt extended by a anyard.

rior to each day's operation, there is a riefing session and inspection of equipment. uring the day, whenever the aircraft is efuelled or shut down, there is a routine -point check of the helicopter, equipment, nd safety gear. The daily routine also ncludes a full debriefing at which discussion s recorded and is often very candid, to say ne least. These sessions are valuable for ointing out potential hazards or improving echnique.

n flight, the clipper operator is responsible or tree selection but the pilot has the final ay on the basis of safety. When agreement on tree is reached, the pilot checks local winds nd moves the aircraft into position while the perator checks the area around the tree for ny hazards and advises on tail rotor learance. As the machine is brought up to ne tree, the operator checks his harness and readies the clipper. When the skid touches the tree stem, the cut is made and top recovered. As the pilot pulls away, the top is stowed in the rear cabin. This is all done in a series of smooth actions with constant communication between pilot and operator. Ten to twelve tops may be clipped during an 8-10 minute cycle. The "what ifs" associated with in-flight clipper problems, loss of communication, injury, or helicopter malfunction are a part of the daily briefing. Anything which occurs that disrupts the smoothness of the operation is considered to be an incident and is discussed at the debriefing.

Aerial clipping is both physically and mentally demanding, so that rest periods for both pilots and operators are rigidly enforced and daily flying times, using two air crews, are the same as for raking. Normally, the Bell 206B (Jet Ranger) is used on the clipping operation.

Clipping is suited to harvesting where the cones are concentrated in the top of the crown. Spruce, especially, is conducive to clipping because practically all the cones are located in the top 3 m (10 ft) of the narrow conical crown. The method is also used effectively on immature Douglas-fir, but when more than one approach to the same tree is necessary, as for true firs or white pine, efficiency declines.

Providing the clipper operator is an agency employee, clipping affords the best opportunity for tree selection on the basis of phenotype, cone ripeness, and the incidence of insect-infested cones. The quality of cones harvested is, therefore, as good or better than when trees are felled or climbed. However, there are disadvantages. The method is not too safe in steep terrain, especially if there is a high frequency of snags. The size of tops which can be harvested is limited to about 2.4 m (8 ft) and to a stem diameter which the clipper will accommodate. Because of rotor wash, holding hover while at the tree is often difficult. The cost of fabricating and installing the clipper unit, preparing the helicopter, and training and outfitting operators is considerable. However, much of this cost is a one-time investment.

AERIAL SYSTEMS IN GENERAL

The use of helicopters provides a little excitement into an activity which, we all know, is far from glamorous. Consequently, we are finding that there is a tendency for the aerial systems to be prescribed for situations where they are not always warranted. People seem to think that aerial systems are the panacea which will end all their problems. This is not so; the criteria for success are demanding.

A collection is measured by the amount of clean seed it yields, so right off the top, high filled-seed counts are a must.

The economic success of the collection operation itself is predicated on maximizing the volume of cones delivered per flying hour. Therefore the crop must be heavy and the species suitable. Present aerial systems are marginal for the cedars and western hemlock and are definitely not suited to ponderosa and lodgepole pine or to western larch. Harvesting is from dominant and codominant trees which have narrow, conical crowns.

Stands should be even-aged and at the peak of their cone-producing years, and should be within about 4 km (2 1/2 miles) of road access or a log landing so that fly-in and fly-out times are short.

Aerial collections require good planning to acquire helicopters and equipment, schedule areas, and to coordinate operations so as to minimize ferry time. Pre-organization is based on a good knowledge of the stand and the surrounding area. This involves a reconnaissance flight to:

a) establish geographical and elevational boundaries;
b) confirm with the pilot the species and types of trees to be harvested;
c) select and check approaches to dump sites and fuelling areas;
d) note hazards to the flying operation such as snags, large birds, powerlines and industrial or recreational activities; and to
e) develop a pattern for harvesting the stand.

The delivery of helicopter fuel is one item i particular that has to be checked; if the tru delivers to the wrong area, you have a costly problem.

Dump and pick sites must be separate from the fuelling area. They must be accessible, firm and free of dust or debris. Helicopter approach and departure paths must be flat and clear of obstructions. A few simple wind-indicators (flagging tape) are desirable

Pickers should not be allowed to work on a landing that helicopters are using. Therefor several dump sites are advisable or the picki can await the completion of the aerial phase. The other option mentioned earlier is to haul the harvested material to a central facility where the pickers can enjoy shelter, and freedom from noise, dust, and bugs. This requires extra monitoring--one person checkin seed set, ripeness, and insect damage at the

Table 1.--Percentage of cones harvested by aerial methods in British Columbia, 1979-83 (registered seed ts only)

Species	1979 Total (Hl)[1]	1979 % Aerial	1980 Total (Hl)	1980 % Aerial	1981 Total (Hl)	1981 % Aerial	1982 Total (Hl)	1982 % Aerial	1983 Total (Hl)	1983 % Aeri
True firs										
Alpine	22.0	-	7.8	-	-	-	18.0	-	-	-
Amabilis	1833.6	91.6	45.8	100.0	-	-	707.8	93.4	350.0	.1
Grand	-	-	13.5	81.5	115.9	100.0	121.3	81.5	25.0	1 .0
Douglas fir										
Coast	621.0	2.9	213.7	-	85.6	-	1431.3	46.1	276.6	-
Interior	311.6	-	822.6	-	-	-	1354.3	13.9	42.0	-
Spruces										
Sitka	1153.2	2.7	1.3	-	0.4	-	2.3	100.0	207.3	.4
Interior	10074.4	8.7	302.4	13.6	-	-	2762.7	48.1	4308.4	.2
Hemlocks										
Western	228.3	4.4	1.0	-	21.1	-	319.9	59.6	11.6	.1
Mountain	83.4	14.3	-	-	-	-	52.2	38.5	5.2	.8
Cedars										
W. red	93.5	-	13.6	-	3.3	-	73.7	19.0	52.6	[illegible]
Yellow	-	-	1.0	-	5.1	-	-	-	1.8	.3
Pines										
Lodgepole	899.3	-	1356.8	-	587.9	-	148.9	-	1020.8	-
Ponderosa	4.0	-	11.8	-	-	-	-	-	50.6	-
W. white	17.5	-	19.6	-	74.0	6.8	32.5	25.2	4.8	1 .0
Larch	-	-	195.7	-	-	-	32.5	-	20.8	-
Total/ Mean	15341.8	20.7	3006.6	3.2	893.3	14.0	7292.3	43.5	6377.5	.7

[1]1 Hl (Hectolitre) = 2.75 (Imp.) = 2.83 (U.S.) Bushels, approx.

dump site, while another monitors cone cleanliness at the picking site.

Aerial harvesting permits collections to be made from areas which are presently inaccessible but likely to be logged in the near future. This means that cones can be processed, seed cleaned, and the stock grown for the area by the time it is logged and prepared. Cone crops can also be harvested from desirable stands which have been reserved for streamside protection or game corridors. Damage to tree crowns and whether or not the mutilated tops become entry points for diseases or insects is also a consideration. Our philosophy is that in most cases, the trees from which cones have been harvested will themselves be harvested in the next few years. In addition, many trees suffer similar damage naturally from snow, ice or wind breakage, and insect populations. Where clipping is used, this consideration is at least minimized by having only one clean cut.

As with any air operation, good weather favors safety and efficiency. Helicopters working in a hover position are particularly sensitive to wind, and to rain when it affects visibility. On cone harvesting operations, winds must be steady and less than 32 km (20 miles) per hour; the ceiling must be at least 150 m (500 ft) above ground; horizontal visibility must be at least 0.8 km (one-half mile) and there must be no impairment due to rain on the bubble.

As mentioned earlier, safety is the controlling factor in any aerial method. We are well aware that if a tragedy occurs on any aerial harvesting operation, then all operations will likely be shut down--at least temporarily--by the federal Ministry of Transport or the Workers' Compensation Board--or both. We believe that this unfortunate situation can best be prevented by:

a) employing certified, capable, and well-trained practitioners;
b) maintaining established and documented procedures backed up by strict discipline;
c) using safe, efficient, and well-maintained equipment; and by
d) continually monitoring the program with debriefings and post-collection "beef" sessions.

EXTENT OF PROGRAM IN BRITISH COLUMBIA

Table 1 outlines the percentages of various species harvested aerially in B.C. during the past five crop years.

Aerial systems have had a high profile (over 90 percent) in the collection of true firs, and are increasing at a steady pace in the harvest of what we call interior spruce which is white, Engelmann, and their natural hybrids. In the last good crop year, over 3800 hectolitres (10,500 bushels) of interior spruce were collected aerially. The reforestation program in B.C. is expanding and will soon reach 200 million trees annually, so it looks like cone harvesting from natural stands will be around for a few years yet.

PRODUCTIVITY

I do not want to discuss dollar costs because they change every year and are meaningless unless the input factors and collection circumstances are similar. Besides, some of our costs would likely make you people south of the 49th parallel shake your heads. Remember, however, that in B.C. we are talking about hectolitres, which are about 2.8 times the U.S. bushel. We are also operating in an economy where we're paying the equivalent of $1.86 for the same gallon of gas that you pay $1.15 for. What we do know is that with aerial collections, there is considerable economy in scale, that is, large collections.

Table 2.--Proportional costs[1] of stand establishment estimated for 1983-84 (108 million seedlings)

Activity	$/1000 seedlings	@ 1150 Seedlings per Hectare[2] $/hectare	¢/seedling	% of total cost
Cone collection	3.00	3.45	0.3	0.5
Seed processing	0.42	0.48	0.04	0.1
Nursery	175.00	201.25	17.5	29.7
Site preparation	166.90	191.93	16.7	28.4
Planting	242.60	279.00	24.3	41.3
Total	587.92	676.11	58.8	100.0

[1] All species, all stock types, all methods; and including production overhead (excluding administration)
[2] Hectare = 2.47 acres (approx.)

Predictably, the costs of delivering the top material to the ground and the shucking and bagging of the cones account for 80-90 percent of the total collection cost. The relative proportion of these two major items appears to depend on cone size and, to some extent, on the size of the branch pieces delivered.

Shucking of true firs is least costly, with Douglas fir, spruce, hemlock and cedar following in that order. In general, clipped tops are easier to pick from because pickers handle only one piece and more cones are intact. Raked material is more fragmented and many smaller pieces must be sorted through.

Our philosophy concerning collection costs is that they are a very minor proportion of the total cost involved in stand establishment. Table 2 indicates that (in 1983-1984) cone collection costs represent about one-half of one percent of the total cost of our restocked hectare.

Actually, the proportion is a bit lower because the seed used has usually been collected and processed in an earlier year when costs would have been less. So we feel that what may seem to be a large increase in collection cost is really only a small increase in total cost of the planted tree. If aerial collection improves seed quality or yield, then we are actually money ahead. Cones from the topmost portion of the crown are likely to have a high seed-set, and the propensity for "selfing" is minimized.

Productivity is best measured by the volume of cones delivered per flying hour, and depends on three factors.

The first, cone volume delivered per cycle, is a function of the:

a) abundance of the crop, (the number of cones per tree and the frequency of cone-bearing trees);
b) the size of the cones;
c) the percentage of cones recovered;
d) the design and efficiency of the equipment;
e) the ability of the air crew; and
f) the size and maneuverability of the helicopter.

The second, elapsed time per cycle, depends largely on the fly-in and fly-out distance. Short cycle times reflect a sound reconnaissance, good pre-organization, and an efficient team operation.

The third factor, picker productivity, is influenced by the species (size) of the cones and the size of the material delivered. The pickers' diligence and attitude is important

Table 3.--Productivity of aerial harvesting (based on data acquired to 1984)

Species	Cone crop Level	Number of collections	Total cones collected (Hl)[1]	Productivity Hl/harvesting hour[2] Lowest	Highest	Average
			Aerial Raking			
Coast D-Fir	Med-Hvy.	3	81.2	-	-	4.3
True firs	Hvy.	13	1663.0	5.7	20.2	14.2
W. hemlock	Med-Hvy.	7	106.2	-	-	2.2
M. hemlock	Med-Hvy.	2	7.8	-	-	3.0
W.R. cedar	Med.	3	13.7	-	-	2.7
Interior spr.	Med.	3	473.2	1.3	2.7	2.6
" "	Hvy.	2	752.4	2.0	3.6	3.4
			Aerial Clipping			
Interior spr.	Med.	3	172.0	2.0	2.2	2.1
" "	Hvy.	5	993.2	3.1	5.3	4.0
Int. D-fir	Med.	3	149.1	1.1	2.7	2.1

[1]1 hectolitre = 2.75 bushels (Imp.) = 2.83 bushels (U.S.) approx.
[2]Clean, sacked cones from material delivered.

and they must be kept happy with a suitable wage, lots of cones to pick, and plenty of bug dope. Picker productivity may be enhanced where material has been hauled to a covered and cool central picking area.

The productivity data we have managed to collect so far provides what we think are fairly credible averages for at least the true firs and interior spruce (table 3). For other species, more information must yet be collected.

Good-sized collections of interior spruce have been made from both medium and heavy crops, and some evidence of the effect of crop abundance is beginning to emerge. We also found that productivity of clipping was higher, and costs lower, after formal training had been given to clipper operators.

At present, we are reasonably pleased with the progress made with aerial harvesting and we are confident that new developments will bring their rewards. The helicopter people have gained considerable experience and have learned a lot about cone picking. We feel that several of the carriers are capable and knowledgeable enough to undertake projects on their own. Accordingly, we are working with them to develop a contract document which will not only meet their needs but also serve the interests of their clients. We are sure that it will all work out just fine.

RECONDITIONING STRATIFIED SEED AT PINE RIDGE FOREST NURSERY

Katherine A. Yakimchuk

ABSTRACT: Lodgepole pine (Pinus contorta) and white spruce (Picea glauca) seed is stratified (moist, prechilling treatment) before sowing at Pine Ridge Forest Nursery, Alberta, Canada, to break dormancy and produce uniform germination. If any stratified seed remains after sowing it can be saved. It should be dried gradually to a storable moisture content (between 4 and 8 percent), placed in a sealed container, and stored at 0°F (-18°C) for later use. Stratified seed that has been reconditioned and stored has maintained its germinability and has produced strong, healthy seedlings.

INTRODUCTION

Lodgepole pine (Pinus contorta) and white spruce (Picea glauca) seed used for sowing at Pine Ridge Forest Nursery is stratified by a moist, prechilling treatment 3 weeks before sowing. Standard practice is to discard any seed remaining after sowing. The assumption is that this seed cannot be stored and maintain high quality. Seed has great value when stocks are low; therefore, it would be ideal to save this seed for future use.

Initial trials on reconditioning stratified seed at Pine Ridge Forest Nursery on five seedlots indicated little or no change in germination. The seedlots have retained their viability after being stored at 0°F (-18°C) for 4 years following stratification and reconditioning. The purpose of this paper is to describe tests of a procedure used for reconditioning stratified seed. This seed has maintained its germinability and has produced strong, healthy seedlings.

METHODS AND MATERIALS

Seed used for testing came from the seed inventory kept at Pine Ridge Forest Nursery. To perform this test, 10.5 ounces (300 grams) of seed were withdrawn from each seedlot. Ten white spruce and one lodgepole pine seedlots originating at various locations in Alberta (table 1) were tested. Germination and moisture tests were performed on the seed before stratification as a control.

Paper presented at the Conifer Tree Seed in the Inland Mountain West Symposium, Missoula, MT, August 5-6, 1985.

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To stratify the seed it was first soaked in distilled water for 24 hours. It was then drained and each seedlot was placed in a plastic screen bag. The seed was spread in a thin layer to a depth of 0.25 inch (6 mm) inside each bag. The bags of seed were placed between layers of damp vermiculite in waxed cardboard boxes. Damp paper towelling was placed around the seed bags so vermiculite particles would not get mixed in with the seed. The seed was stored at 40°F (4.5°C) for 21 days. After 21 days the seed was removed from storage and a 0.5 ounce (15 gram) sample was taken from each seedlot for germination and moisture testing.

The remaining seed was air dried by pouring each seedlot out of its mesh bag onto a tray, and spreading it into a thin layer. An oscillating fan was placed by the seed to assist drying. The seed was dried for 15 to 20 minutes, until no surface moisture was visible. This is the condition of seed used in regular nursery sowing operations. A 0.5 ounce (15 gram) sample was taken from each seedlot for germination and moisture testing.

The seed remaining on the trays was left to dry for 3 days at room temperature, until it reached a storable moisture content of 6 to 8 percent. After this drying process, a 0.5 ounce (15 gram) sample was taken from each seedlot for germination and moisture testing.

Seed remaining was sealed in plastic bags and placed inside waxed cardboard boxes for storage in seed freezers at 0°F (-18°C). Following this the seed was sampled each month for germination and moisture testing to assess its quality.

Testing followed International Seed Testing Association rules (International Seed Testing Association 1976). Moisture content was analyzed using two 0.18 ounce (5 grams) replicates of seed each. The seed was oven dried at 220°F (105°C) for 16 hours. The percent moisture content was calculated on a wet-weight basis. Germination tests were made by placing the seed on moist kimpac paper towelling inside covered, clear, polycarbonate trays. Four replicates of 100 seeds each were used per test. Test seeds were germinated in Conviron germination cabinets for 21 days at 77°F (25°C) with a 12-hour photoperiod. Germination counts were made twice per week using the vigor class system developed by Wang (1973). During seedling evaluations, only the vigor class 1 seedlings were removed from the trays. The remaining seedlings were left to develop further.

Table 1.--Origins and collection years of seed samples used from the Alberta seed inventory for reconditioning tests

Seedlot	Species[1]	Collection year	Township	Range	Meridian	Longitude (°W)	Latitude (°N)
			Location				
1	Sw	79	110	16	5	116° 45'	58° 35'
2	Sw	75	94	11	4	111° 50'	57° 10'
3	Sw	82	80	25	4	114° 05'	55° 55'
4	Sw	83	80	25	4	114° 05'	55° 55'
5	Sw	79	77	11	6	119° 55'	55° 45'
6	Pl	82	66	10	5	115° 45'	54° 45'
7	Sw	79	62	20	5	117° 25'	54° 25'
8	Sw	82	43	10	5	115° 45'	52° 45'
9	Sw	79	41	15	5	116° 35'	52° 35'
.0	Sw	79	35	8	5	119° 25'	52° 0'
.1	Sw	71	8	4	5	114° 45'	49° 40'

'Sw = white spruce, Pl = lodgepole pine

'inal germination percentages were calculated to . vigor class 4. At Pine Ridge Forest Nursery it s felt that a seedling not having reached this ;ize in 21 days will not survive in the field or [reenhouse. Vigor classes used are as follows:

1. Normal, fully developed seedlings with ;eedcoat completely shed.
2. Normal, well-developed seedlings with ;eedcoat almost shed.
3. Normal, well-developed seedlings with 'isible cotyledons and seedcoat partly shed.
4. Normal seedlings with moderately developed ıypocotyl and cotyledons barely visible.

ınalysis of variance was performed on the [ermination test data for each treatment. ;ermination percentages calculated to vigor class · and vigor class 2 were analysed. Duncan's ıultiple range test was run to test the differences n germination among treatments.

'isual assessments of seedling growth were made luring seedling counts. These were based on ıeight, strength, color, and uniformity of [rowth among all seedlings.

RESULTS AND DISCUSSION

Visual assessment showed that seedlings from the control (no treatment) for all seedlots were strong and healthy but showed an unevenness of growth. Heights of seedlings within each replicate varied. Seedlings from stratified seed showed uniformity in height and were generally tall, strong, and healthy. This was seen at the onset of the trial as well as after the seed had been kept in cold storage.

The initial moisture content of all but one seedlot was between 5 and 7 percent (table 2). After stratification, moisture contents increased to 31.4-34.5 percent. When the seed was air dried for removal of surface moisture, moisture contents were lowered to 28.6-32.2 percent. After air-drying the seed for 3 days, moisture contents were reduced to 5.9-7.7 percent. This is the recommended moisture content for long-term storage of white spruce and lodgepole pine seed (Wang 1974). The seed retained this moisture content during the time it was kept in storage.

'able 2.--Moisture content (percent) of 11 Alberta white spruce and lodgepole pine seedlots after four treatments

;eedlot	Control	Wet	Air Dry	Dried for storage	Stored for 1 year
		Treatment			
1	6.0	31.4	29.7	7.7	7.0
2	3.8	33.1	31.1	6.3	6.5
3	5.6	31.9	31.5	6.6	6.6
4	6.3	32.6	29.0	5.9	6.2
5	5.9	31.3	30.1	6.9	6.8
6	6.3	34.5	32.2	7.7	7.6
7	5.7	31.9	30.5	7.5	7.2
8	5.2	32.5	28.6	6.1	6.4
9	6.4	34.1	31.5	7.7	7.3
.0	6.1	32.9	30.9	7.6	6.6
1	5.7	32.9	31.9	6.1	6.3

Analysis of variance at a 5 percent confidence level, based on germination results to a vigor class 4 and 2, indicated that eight of the 11 seedlots showed significant differences among treatments. In most of these cases, the control germination percentages are lower than those of the treated seeds. This indicated that stratification is necessary for maximum germination. Germination percentages varied very little among the stratified, air dried, and dried-for-storage trials. Sampling and testing the seed monthly while it was in storage indicated that the germination percentages for most of the seedlots remained very close to the original stratified percentages. For seven seedlots, the analysis of variance indicated there was a significant difference in germination in the last months of storage. Viability of the seed may have been deteriorating, but the seedlings produced from these seedlots were still very strong and healthy. Five of the seedlots that showed a reduction in germination had a lower germination percent originally. The other seedlots appear to be just as vigorous after being kept in storage as they were at the star[illegible] of the trials.

By comparing germination percentages to vigor classes 2 and 4 (table 3), it is evident that the seed has retained its germination capacity as the seed germinated quickly and reached an acceptable size in 21 days. The majority of the seedlings reached the vigor class 2 size within 21 days.

The germination data show that stratifying the seed, drying it, and storing it at 0°F (-1[illegible]°C)

Table 3.--Comparison of germination (percent) of 11 Alberta white spruce and lodgepole pine seedlots after four treatments and seven storage times[a]

Seedlot	Control[b]	Wet[c]	Air Dry[d]	Dry[e]	Storage time (months) 2	3	4	5	6	7	8	9	10	11	1[illegible]
				GERMINATION TO VIGOR CLASS 4 IN 21 DAYS											
1	86[2]	91	90	86	93	90	88	90	91	89.5	91	90.5	86[7]	87[1]	[illegible][6]
2	68[6]	82	82	83	80.5	76.5	75	76	78.5	76	77.5	72[3]	69[5]	72[3]	[illegible].5[6]
3	67[2]	78.5	77	72	73	74	70.5	73	74.5	75	72	70[1]	66[2]	67[2]	[illegible][2]
4	67[4]	80	77	74	77.5	74	67.5[4]	70.5[1]	76	65[6]	68[4]	67.5[4]	66.5[4]	67[4]	[illegible][1]
5	88.5[11]	96	94	94	96	95	93	94.5	96	92	91[3]	94	92	93	[illegible]
6	93	94.5	96	94	93	93	91	95	93	92	92	92.5	95	95	[illegible]
7	48.5[14]	72	67	65	70.5	63[1]	62[2]	59[2]	64.5	59[2]	60[2]	62.5[1]	59.5[2]	62[2]	[illegible]
8	91.5[8]	97	95	97	96	94	94	95	96	96.5	97	96	94.5	93[2]	[illegible][3]
9	79	83	81	80.5	80	72[5]	74[1]	76	79	75[1]	81.5	77.5	75[1]	72[6]	[illegible][1]
10	75	81	76.5	74.5	76	76	78	74	73	72	70	70	73.5	78	[illegible]
11	81	84	83	82	86	84	79	82	81.5	84	78	83	82.5	85	[illegible]
				GERMINATION TO VIGOR CLASS 2 IN 21 DAYS											
1	80	90	90	85	91.5	87.5	85	88	90.5	86	86	88.5	83.5	85.75	[illegible]
2	52.5[7]	64.5	60[4]	68	74.5	66.5	58[4]	59[4]	71.5	72.5	72	45[11]	51.5[7]	61.0[2]	[illegible].75
3	60.5[4]	71.5	74	69.5	67	71	68	68.5	71	68	67	65.25	58.75[7]	61.75[4]	[illegible].75
4	59[6]	77	74.5	72	73.5	70	64[3]	67.5[1]	72.5	64[4]	66[1]	61.25[5]	61.5[5]	62.25[5]	[illegible][2]
5	83[13]	94	93.5	93.5	94	93	91	91.5	94	88.5[4]	87.5[3]	89.5	89	93	[illegible].25
6	92	93.5	95.5	93.5	92.5	92	91	94	92.5	89.5	91.5	92	94.75	94.5	[illegible].75
7	46[14]	64.5	64	62	68	57.5[1]	57.5[1]	53[3]	61.5	55[3]	56.5[1]	54.25[3]	54.5[3]	57.25[1]	[illegible].75
8	90.5	95	95	95	94	90	91.5	93.5	95	94.5	94.5	92.25	92	92	[illegible]
9	71[2]	80.5	80	78	78	71.5[2]	72	70[2]	77	72	78	72.5	71.75	67.75[6]	[illegible].5
10	64.5[6]	77	76	72.5	75	72.5	74.5	67[3]	69.5	64[7]	63[7]	68.5[1]	68.75[1]	74.5	[illegible].25
11	69[11]	80	81	80	83	81	73.5[1]	79	80	81.5	75	78.25	78.75	79	[illegible].5[2]

[a] Raised numeral in table indicates number of times treatment is significantly lower than others in the trial at a 5 percent level determined by Duncan's multiple range test.
[b] No treatment.
[c] Stratified seed before air drying.
[d] Seed air dried for removal of surface moisture.
[e] Seed dried to a moisture content of 6-8 percent.

does not destroy seed quality. All seedlots reacted similarly, regardless of their origin in Alberta.

CONCLUSIONS

1. White spruce and lodgepole pine seed must be given a moist prechilling treatment before sowing, to attain maximum germination and uniform growth.
2. Stratified seed that has not been sown should be dried down gradually to a moisture content of about 6 percent, sealed in a container, and stored at 0°F (-18°).
3. Reconditioned seed should be used within 1 year to ensure high quality. Some seedlots may have lower germination, as determined by periodic testing, after being reconditioned and stored for several months. Seed should be used as soon as possible.
4. Seedlots that initially have lower germination potential deteriorate sooner than seedlots having high germination potential.
5. Saving unused stratified seed eliminates waste of costly seed, especially in areas where the seed inventory is low.
6. Testing will continue to determine whether reconditioned seed can be stored longer than 1 year and still maintain its viability.

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Section 3. Seed Orchard and Seed Production Area Management

REVIEW OF SEED PRODUCTION AREA AND SEED ORCHARD

MANAGEMENT IN THE INLAND MOUNTAIN WEST

Jenji Konishi

ABSTRACT: Based on survey data from various agencies in the Inland Mountain West, which covers that region between the east slopes of the Cascade Mountains, the Rocky Mountains, through to the Plains, the current scale of the planting program is identified. The proportion of cones collected for various species from natural stands, seed production areas, and seed orchards is estimated.

Current practices in cone crop induction, cone and seed pest control, and cone harvest and processing methods employed to procure the necessary seed supply are reviewed.

The future trend for certain portions of the Inland Mountain West region is to establish and intensively manage seed orchards to produce seed of superior genetic quality for the major reforestation species.

INTRODUCTION

The area surveyed to address my topic includes the three (3) western Canadian provinces and thirteen (13) of the western and mid-western states of the United States (fig. 1). The area west of the Cascade Mountains has been excluded for the purposes of this review.

Within the Inland Mountain West Region the current annual planting program is estimated to total 201,681,000 trees. The total planting in the Canadian portion of the Region is 127,333,000 trees, and in the 13 states 74,348,000 trees (table 1).

This Region is characterized by diversity in climate, terrain, and economically important conifer tree species.

Paper presented at the Symposium on Conifer Tree Seed in the Inland Mountain West, Missoula, MT, August 5-6, 1985.

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Figure 1.--Inland Mountain West Region (The dashed line marks the divide of the Cascade Mountains).

The major species planted in the provinces are engelmann and white spruce, lodgepole pine, Douglas-fir and jack pine (table 2). The major species planted in the states are Engelmann spruce, Douglas-fir, ponderosa, lodgepole, white, and sugar pine, grand fir, and larch.

Table 1.--Production of tree planting stock for the Inland Mountain West Region

Region Area	Production	
USA (1984)		
Arizona	190,000	
California	10,000,000*	
Colorado	2,716,000	
Idaho	25,349,000	
Montana	2,643,000	
Nevada	237,000	
New Mexico	7,641,000	
North Dakota	3,558,000	
South Dakota	1,734,000	
Oregon	10,000,000*	
Washington	10,000,000*	
Utah	280,000	
Wyoming	No data	
Total 13 states		74,348,000
Canada (1985)		
British Columbia	87,000,000*	
Alberta	30,333,000	
Saskatchewan	10,000,000	
Total 3 provinces		127,333,000
Total estimated planting - Inland Mountain West Reg.		201,681,000

*Estimates for east of Cascades

For source of data see references.

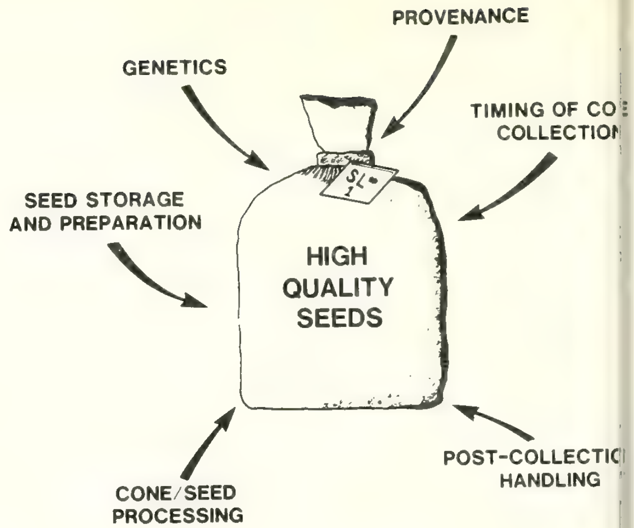

Figure 2.--Factors contributing to high seed quality.

For the provinces, based on the above species ratio and planting rate, a total of approximately 3405 hectolitres of cones (9,350 bushels) are required to annually sustain a program of this scale. These cone volumes do not consider needs of direct seeding programs in Alberta and Saskatchewan. Considering the species mix for the mid-western states it is estimated that an equivalent volume is needed t sustain the United States' portion of the program in this Region.

In order to meet the above demands a systematic approach to seed procurement was undertaken. I included the establishment and management of seed production areas (SPA's) and seed orchards. The objective of these concepts was to secure and provide high-quality seeds (fig. 2) needed for the expanding planting programs. In some of the species, collectible

Table 2.--Major species planted in western Canadian Provinces (millions of trees sown for in nurseries - 1985)

	Spruce (White & Engelmann)	Lodge-pole Pine	Douglas-fir	Jack Pine	Other Species[1]	Totals
B.C.[2]	56.5	22.0	5.1	-	3.4	87.0
Alberta[3]	26.0	4.2	0.1	-	-	30.3
Sask.[4]	6.3	-	-	3.7	-	10.0
Totals	88.8	26.2	5.2	3.7	3.4	127.3
	69.7%	20.6%	4.1%	2.9%	2.7%	100.0%

1 Other species includes Western Red Cedar, Western Larch, Western White Pine and Ponderosa Pine.
2 Silviculture Branch, Ministry of Forests, Province of B.C., Victoria. Excludes planting west of Cascade Mountains.
3 Reforestation and Reclamation Branch, Energy, Mines and Natural Resources, Province of Alberta, Edmonton.
4 Forestry Division, Parks and Renewable Resources, Province of Saskatchewan, Prince Albert.

cone crops occur at infrequent intervals in natural stands. For example, in British Columbia, seven collectible interior spruce cone crops have occurred during the past 26 years (fig. 3). This equates to a collectible crop every 3.7 years but experience indicates there can be intervals for up to 10 years between collectible crops. Cone crop periodicity in some species makes procurement of a sufficient inventory of seeds difficult.

SOURCES OF SEEDS

Over the past 20 years, most provinces, states and larger private land agencies within the region have established SPA's for the major planting species (Appendix I). In general, SPA's have been established to produce seed in the interval required to establish seed orchards and bring them into production.

Seed orchard programs have been implemented recently (within the last 10 years) in the interior region of B.C. and Alberta, and are in the planning stage in Saskatchewan. In the western states, orchards have been established in some areas for those species with larger planting demands (Appendix II). Over the next 10 - 20 years as established orchards mature and additional orchards are planted, this concept will significantly increase as a source of genetically improved seeds for future reforestation programs.

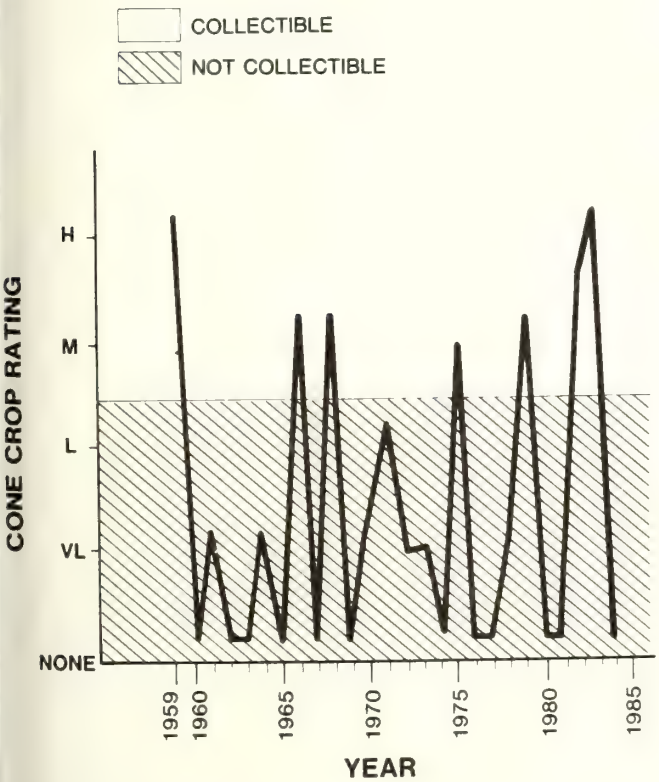

Figure 3.--Spruce cone crop rating 1959-1984, central interior region of British Columbia.

Based on a Canada-wide tree seed survey (for 1980-81) by P. S. Janas and B. D. Haddon over 88% of seed used for major reforestation species originated from unimproved natural stands, slightly over 11% came from seed collection and seed production areas and only 0.2% was from seed orchards. A similar pattern exists for the provinces within the Inland Mountain West Region. Data of this nature were not obtained from the Western States, but again, a similar distribution in terms of source of seeds is suspected.

In summarizing, despite the establishment of SPA's and orchards over the past 20 years, the majority of cone collections are currently being harvested from unmanaged natural stands.

In some provinces and states, provenance tests have been established and reviewed (10 years+ after establishment). For example, in B.C. a review of provenance tests for interior spruce and lodgepole pine has resulted in the revision of seed zonation and transfer rules as well as the identification of superior provenances to serve as priority areas for operational cone collection (figs. 4 and 5). It is of interest to note that in both spruce and lodgepole pine some of the best-performing provenances originated from low to middle elevation in the moist transition zone between the dry and wet interior forests west of the Rocky Mountains.

MANAGEMENT PRACTICES - SPA'S

Stand Selection

Stand selection has for the most part been done without the benefit of advance provenance testing work. Some of the criteria used for selection can be listed:

(a) thrifty young stands (25 - 30 years+) with good tree form,

(b) appropriate geographic and elevational distribution within a seed planning zone,

(c) gently sloping terrain and south facing aspects are preferred, and

(d) stand should be accessible by all weather road.

Roguing, Thinning, and Brush Control

Selected stands are brushed out to reduce weed competition and thinned and/or rogued of overstocked stems. Inferior phenotypes are removed to enable genetic improvement both within the SPA and within a perimeter buffer strip (usually 5 times the average tree height in width) to serve as a pollen isolation zone.

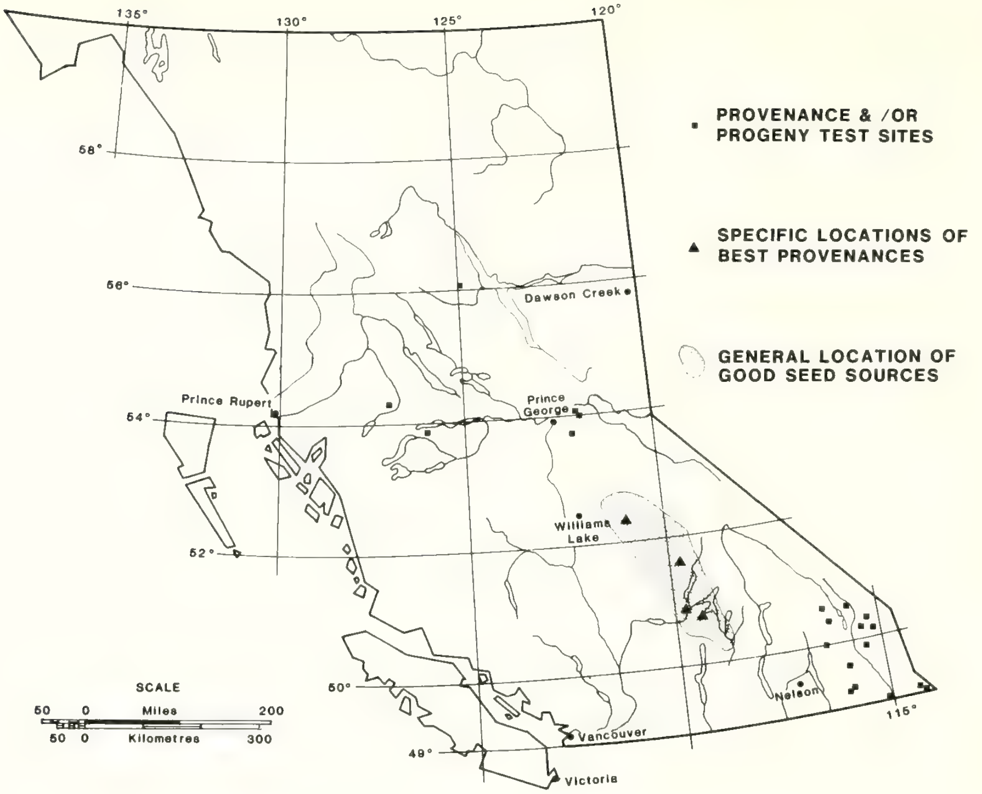

Figure 4.--Interior spruce provenance and progeny test sites and location of good seed sources.

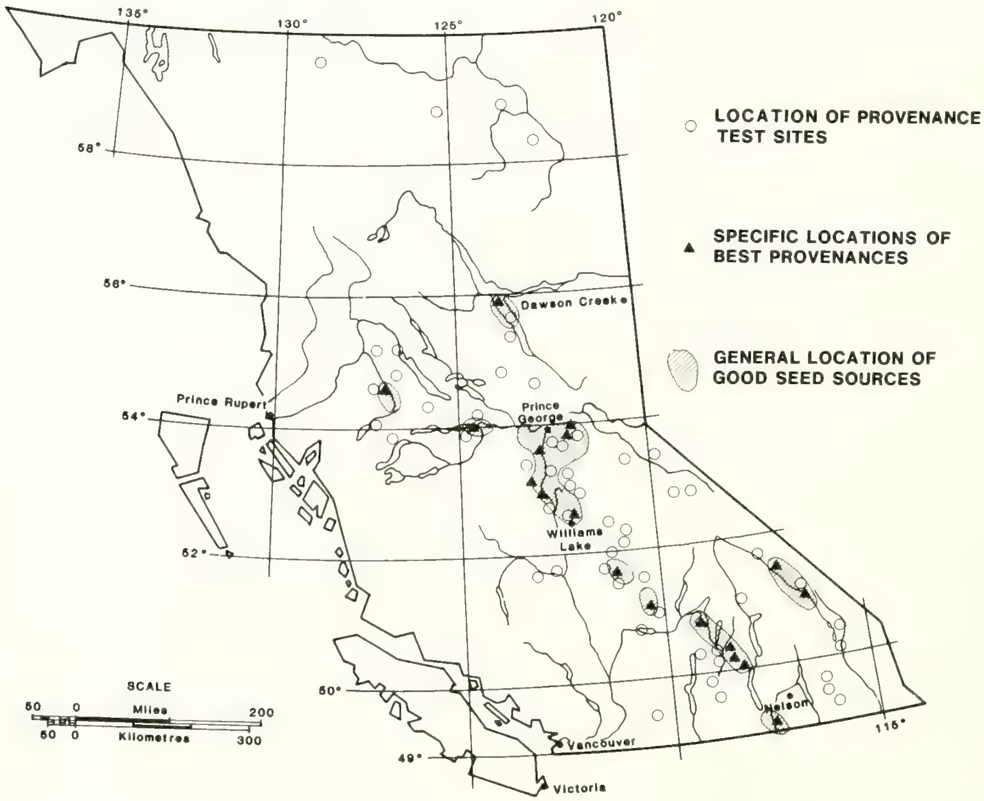

Figure 5.--Lodgepole pine provenance test sites and location of good seed sources.

In thinning, care needs to be exercised to prevent windthrow and sunscalding of residual trees.

Thinning provides for free growing trees which produce large crowns conducive for optimizing cone production. It also provides for access by equipment for cultural and protection operations.

Fertilizing

To improve the nutritional status of the soil and the trees and to induce cone production, fertilizer applications are made usually in the form of ammonium or calcium nitrate. Fertilizing is done manually, by tractor powered equipment, and in some instances, by aircraft. In British Columbia, despite fertilizing treatments in interior Douglas-fir and interior spruce SPA's the response in terms of cone induction has been inconsistent.

Protection

During brushing and thinning operations the resulting slash is disposed to reduce the fire hazard. It is also important that forest land management staff are advised of the location of SPA's so that they can be protected where possible from fires and/or land alienation for rights-of-ways or for other purposes.

Experiments to control cone and seed pests on SPA's have been limited and the results inconsistent.

Cone Harvest

Cone harvesting is usually done by climbing. In some SPA's where the trees have grown tall the tops have been removed at time of cone harvest.

Summary of Current SPA Performance

In some species such as ponderosa, lodgepole, and white pine, seed production from SPA's has been consistent. In many of the other major species such as engelmann and white spruce, Douglas-fir, and larch, production has been sporadic. In B.C. only one or two cone collections have been made from the interior spruce and Douglas-fir SPA's established 20 years ago. Where poor seed production has been experienced, the concept needs to be evaluated and perhaps phased out. In some instances it is doubtful that the costs of SPA establishment and management can be justified in light of the low seed production and limited genetic improvement resulting from this approach. In the survey, an attempt was made to gather seed yield data from SPA's. While many returns were received there exists a scarcity of yield data. This recent experience in data collection was also echoed previously (1974) by Paul Rudolph, Keith Dorman, Robert Hitt and Perry Plummer in Chapter III, Production of Genetically Improved Seeds, U.S. Woody Plant Seed Manual.

MANAGEMENT PRACTICES - SEED ORCHARDS

Planning

Where large scale planting programs are to be sustained over a long term, seed orchard programs have been implemented and/or are under consideration to provide both abundant quantities of seeds as well as superior genetic quality.

Long-term forecasting of species planting requirements (20 - 50+ years) is fundamental to priorizing tree breeding and seed orchard projects for a species. To optimize genetic gains it is essential that orchard programs be integrated with breeding programs.

Tree breeding and associated seed orchard programs represent a substantial long-term investment where the returns are not realized until harvest of the next forest crop. In view of this point, it is important when implementing a tree improvement program for a species that favourable cost-benefit studies be provided to ensure long-term and sustained support from financial authorities (i.e., Government or forest company).

Once the orchard project is decided upon further decisions must be made as to the type of orchard to establish (i.e., seedling vs. clonal). Experience in coastal Douglas-fir indicates that seedling orchards outproduce clonal orchards 2:1. The generation of orchard needs to be selected (1st vs. 1.5 vs. 2nd generation orchard). An orchard design must be prepared to define tree spacing and clonal or family arrangement to enable optimal panmixia. An orchard working plan document which covers the above topics as well as those which follow can aid orchard staff in management operations.

Within the region surveyed orchard management varies from extensive to intensive. The points which follow apply to intensive management.

Site Selection

Orchard site selection is of crucial importance in that it can determine the success or failure of the project. Some important factors to consider are listed:

(a) climate - warmer and drier site than that of the parent tree's site region. Avoid sites which are subject to late spring or early autumn frosts.

(b) soil and topography - well drained soils on level to very moderate sloping ground which can be easily worked by equipment should be selected. Avoid sites characterized by strong prevailing winds.

(c) services and economy of scale - to enable efficient management of the orchard the following points need to be considered:

(i) availability of an abundant suitable water supply,

(ii) good access road and close proximity to hydro, labour, equipment and supplies,

(iii) plan for enough orchards to be located on a site to justify capital improvements; orchards in combination with nursery operations also assists in meeting economy of scale.

(d) freedom from pests - areas free of known pests and diseases should be selected. For example, root rots and tree rusts can cause problems.

(e) isolation - the site should be isolated from foreign pollen and also from residential areas and lakes or streams which may restrict use of pesticides within the orchard.

Irrigation

Most orchards are equipped with either drip or solid-set irrigation systems.

A drip system is cheaper than the overhead system and requires much less water. The irrigation line can be either laid on the surface or buried.

The solid set system can be used to cool the orchard in the spring and thereby delay the flowering of orchard stock. This delay in flowering can reduce pollen contamination (where the same species occurs adjacent to the orchard) as well as risks from frost and cone and seed insect damage.

Drainage, Site Preparation, and Cover Crop Establishment

The orchard site should include installation of water drainage systems where required. The soil should be well prepared prior to planting to permit good drainage and allow optimal root development. Establishment of a cover crop can aid in controlling erosion and reduce soil compaction and add organic matter.

Soil and Tissue Analysis and Fertilizer Prescriptions

Soil analysis should be completed early in the planning stage to determine nutrient status levels and pH. Examination should also be made for soilborne pests.

Soon after orchard stock is planted, twig and needle samples should be taken at a specific time each year (e.g. early October in B.C. orchards) and the tissue material analyzed at a laboratory. This data should then be interpreted to develop appropriate fertilizer prescriptions to keep orchard stock in a healthy and vigorous condition at all times.

Pruning

Pruning may include removal of small inter-nodal branches in some species to improve light penetration and aeration. Top pruning may be required to control height where orchard irrigation systems are installed and to minimize cone picking height.

Cone and Seed Pest Control

A sound knowledge of and the ability to identify pests at an early stage as well as availability of effective pesticides and control methods are basic to controlling loss of seeds from pests.

As cone and seed insects can be one of the major sources of seed loss, consideration should be given to organizing conelet sampling and analysis for each orchard to determine insect infestation levels as conelets develop. Accurate assays done at the right time can assist the orchardist in deciding whether to spray or not to spray for control.

Sanitation practices include picking all the cones from the trees regardless of crop size. Leaving cones on trees and allowing them to drop to the ground only serves as a brooding base to increase insect populations.

Pollen Handling

Techniques have been developed to harvest, extract, store, test, and reapply pollen on orchards. This enables improvement of the genetic makeup as well as yield of seeds, especially in the early phase of seed production. Once sufficient within-orchard pollen is produced wind pollination is sufficient, however, booster pollination to the very early and late flowering trees can optimize seed set. To be of benefit it is most important that pollen be applied when flowers are in the optimal receptivity phase of conelet development, (i.e., just after bud burst).

Cone Induction

While choosing the appropriate site for orchard location can provide abundant and frequent cone production, experience indicates that many trees in an orchard do not produce cones at the frequency and quantities desired. Consistent annual or biennial seed production of all trees is desirable.

Some treatments being used operationally and/or experimentally to induce cone production include root pruning, girdling, fertilizing, and application of gibberlic acids.

Cone Harvesting

Most cone harvesting in orchards is done with the aid of ladders. In some orchards, hydraulically operated man-lift units used in the fruit industry are also utilized in seed orchards. These units have a slow ground speed but are versatile in that they can be used for conducting orchard surveys, enable pruning, pest control and pollination as well as for cone harvest.

Alternatives to Conventional Orchards

Field orchards require careful site selection, investment in land area sufficient to enable economy of scale of operations and 10 - 15 years are required prior to production of significant quantities of seeds. Container-based seed orchards in greenhouses can accelerate abundant and early seed production, reduce the land area required and may be a cost effective alternative to field-based orchards.

Another alternative is hedging orchards whereby selected superior clones are established in hedges to serve as cuttings for asexual production of planting stock.

Summary of Current Orchard Programs and Performance

In the provinces, orchards are in the very early stage of production and many orchards are under development or in the planning stage. Early production experience in lodgepole pine indicates that orchards can consistently produce seeds germinating at 95%+ and the seeds are larger than those from natural stands. In the North Idaho and Montana area most of the seed production to date is rust resistant white pine. Many other orchards are established or under development for the other major reforestation species. Based on survey returns orchards have not yet been established in Colorado, South Dakota, Wyoming, Arizona, New Mexico, Utah and Nevada. In these states the scales of the planting programs are considered too small to develop an economic tree improvement and orchard program. Also, for this area, much reliance is placed on natural regeneration. In the Pacific-northwest area (east of Cascade Mountains) in Washington and Oregon the main production to date has been in blister rust resistant white pine. Early seed production is being experienced in grand fir, Shasta and white fir, larch, ponderosa, sugar, and lodgepole pine, and many orchards are in the development stage. In this area it is intended that as seed orchards produce sufficient seeds to meet program needs the SPA's will be phased out.

It is most important that seed orchard programs be integrated with tree breeding programs and/or utilize the information provided by thorough provenance studies for a species. In this way maximum genetic improvement of the seed produced is realized.

While many seed orchard management practices have been developed during the past 20 years there exist opportunities for improvement in the following areas:

- genetic quality improvement through early establishment of 1.5 or 2nd generation orchards linked to long-term breeding plans,

- carefully evaluate the performance of 1st generation orchards and from this experience make improvements in orchard site selection, and in design of 1.5 or 2nd generation orchards so that both genetic gain and seed productivity is optimized,

- a significant increase in orchard development and establishment is needed forthwith if orchard seed is to be the major source of seeds for future planting programs,

- expediting earlier seed production through development of new techniques such as containerized orchards,

- establishment of hedging orchards which serve to produce rooted cuttings,

- research is required on cone induction to ensure that all trees produce abundant and regular crops, and

- research is required on pests and their control to minimize loss in orchards.

ACKNOWLEDGMENTS AND CONCLUDING REMARKS

In concluding I wish to thank the organizers of this important symposium for the opportunity to review SPA and seed orchard management in the Inland Mountain West. I also wish to thank those persons who responded to my questionnaire on SPA's and seed orchards. I am sure this symposium and the resulting proceedings will contribute most significantly towards extending knowledge of seed biology, of operational cone collection and seed handling practices as well as management of SPA's and seed orchards. I cannot overemphasize the importance of knowledgeable, well-trained, enthusiastic and dedicated silviculture staff in meeting the objective of supplying high-quality seed for forest renewal programs.

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APPENDIX I

Inland Mountain West Seed Production Areas (SPA's)

Species[a]	No. SPA's	Area (ha/ac)	Seed Produced to Date (kgs/lbs)	Ave. Annual Amount Seed Production (kgs/lbs)	Agency
CANADA - (Metric)					
British Columbia (East of Cascades)					
Fdi	21	-	-	-	MOF
Lw	1	-	-	-	MOF
Py	2	3949.2	-	-	MOF
Pw	1	-	-	-	MOF
Pl	2	-	-	-	MOF
Se	9	-	-	-	MOF
Sx	53	3478.3	-	-	MOF
Totals:	89	7427.5	b		
Alberta					
No SPA's considered to be active.					Government
Saskatchewan					
Sw	5	52.0	15.6	4.0	Government
Grand Total Western Provinces	94	7479.5	-	-	
USA - (Imperial)					
Region 1 - Northern Region - USDA (N. Idaho, W. &. Cen. Montana)					
Fdi	40[c]	842	57.4	14.4	Nat. Forest
Lw			4.6	1.2	Nat. Forest
Pw			85.1	21.3	Nat. Forest
Pl			11.8	2.9	Nat. Forest
Pw	1	6	0.0	0.0	Montana State
Totals:	41	848	158.9		
Region 2 - Rocky Mountain Region - USDA (Colorado, South Dakota, Wyoming)					
Py	5	95	535	134	Wyoming State
Pl	1	4	0	0	Colorado State
Py	1	142	-	-	Nat. Forest
Py	1	40	-	10.4	Nat. Forest
Totals:	8	281			

[a] See Appendix III for species abbreviations.
[b] Minimal collections made each year.
[c] Fdi and Lw will predominate.

APPENDIX I (Cont'd)

Inland Mountain West Seed Production Areas (SPA's)

Species	No. SPA's	Area (ha/ac)	Seed Produced to Date (kgs/lbs)	Ave. Annual Amount Seed Production (kgs/lbs)	Agency
USA - (Imperial)					
Region 3 - Southwestern Region - USDA (Arizona, New Mexico)					
No SPA's - candidate areas are anticipated to be submitted for review and approval in the next few years.					
Region 4 - Intermountain Region - USDA (S. Idaho, Utah, Nevada)					
Fdi	2	18	-	-	Nat. Forest
Py	11	100	-	-	Nat. Forest
Pl	1	-	-	-	Nat. Forest
Totals:	14	118			
Region 6 - Pacific Northwest Region - USDA (Washington, Oregon - East of Cascades)					
Lw	5	22	-	-	Nat. Forest
Py	2	5	-	-	Nat. Forest
Pl	1	22	-	-	Nat. Forest
Se	1	15	-	-	Nat. Forest
Totals:	9	64			
Grand Total USA	72	1311			
Grand Total Inland Mountain West (Can. & USA)	166				

Inland Mountain West Seed Orchards

Species	Stage of Orchards[a] (No. - ha/ac) Dev.	Est.	Prod.	Totals	Total Seed Produced to Date (kgs/lbs)	Ave. Ann. Cur. Seed Production (kgs/lbs)	Agency
CANADA - (Metric)							
British Columbia (East of Cascades)							
Pli	2- 8.6	4-14.7	-	6-23.3	5.62	1.87	MOF
	1- 5.0		-	1- 5.0	-	-	Co-op.[b]
Sx	2- 7.7	8-23.6	-	10-31.3	2.32	-	MOF
	1- 7.4	2- 5.6	-	3-13.0	-	-	Co-op.
Totals:	6-28.7	14-43.9	-	20-72.6			
Alberta							
Pl	1-14.7		-	1-14.7	-	-	Co-op.
Sw	2- 3.5	1- 2.5	-	3- 6.0			Co-op/F.S.
Totals:	3-18.2	1- 2.5		4-20.7			
Saskatchewan							
No Seed Orchards established to date.							
Grand Total Western Provinces	9-46.4	15-46.4	-	24-93.3			
USA - (Imperial)							
Region 1 - Northern Region - USDA (N. Idaho, W & Cen. Montana)							
Fdi	5-37	-	-	5- 37	0	-	Nat. Forest
Bg	-	2- 30	-	2- 30	0		Nat. Forest
Lw	1-10	2- 24	-	3- 34	1.5		Nat. Forest
Py	-	4- 80	-	4- 80	0		Nat. Forest
Pw	1- 4	1- 16	5-80	7-100	275	40	Nat. Forest
Pl	2-20	-	-	2- 20	0		Nat. Forest
Py	-	1- 12	-	1- 12	few cones	-	B.of L.M.[c]
Fdi	1-12	-	-	1- 12	0		State Forest
Lw	1- 8	-	-	1- 8	0		State Forest
Py	-	1- 12.5	-	1- 12.5	0		State Forest
Blue Spruce	1- 3	-	-	1- 3	0		State Forest
d	1- 3	-	-	1- 3	0		State Forest
Totals:	13-97	11-174.5	5-80	29-351.5	276.5		

[a] Classification — Stage
- Developing — site clearing or preparation and/or under propagation.
- Established — 80%+ planted.
- Producing — orchards that have produced greater than 40% of seed target in any one year.

[b] Co-op = in British Columbia, cooperative seed orchards managed by forest companies under government funding.

[c] Bureau of Land Management.

[d] Russian Olive, Siberian Elm, Green Ash.

APPENDIX II (Cont'd)

Inland Mountain West Seed Orchards

Species	Stage of Orchards[a] (No. - ha/ac) Dev.	Est.	Prod.	Totals	Total Seed Produced to Date (kgs/lbs)	Ave. Ann. Cur. Seed Production (kgs/lbs)	Agency
USA - (Imperial)							
Region 2 - Rocky Mountain Region - USDA (Colorado, South Dakota, Wyoming)							
No established Seed Orchards in these states.							
Region 3 - Southwestern Region - USDA (Arizona, New Mexico)							
No known Seed Orchards in the private sector, or municipalites of New Mexico or Arizona.							
Region 4 - Intermountain Region - USDA (S. Idaho, Utah, Nevada)							
No Seed Orchards established.							
Region 6 - Pacific Northwest - USDA (Washington, Oregon - East of Cascades)							
Fdc	48- 465	-	-	48- 465	2898	3.4	Nat. Forest
Bg	3- 27	-	-	3- 27	-	8.9	Nat. Forest
Bsr	1- 9	1- 12	-	2- 21	-	6.8	Nat. Forest
Bw	9- 134	2- 14	-	11- 148	-	5.5	Nat. Forest
Lw	16- 172	-	-	16- 172	-	1.3	Nat. Forest
Py	51- 927	8-110	-	59-1037	-	8.9	Nat. Forest
Pw	8- 91	1- 10	-	9- 101	426	13.1	Nat. Forest
Pl	25- 351	1- 11	-	26- 362	-	2.4	Nat. Forest
Ps	2- 34	-	-	2- 34	-	21.6	Nat. Forest
Se	1- 7	-	-	1- 7	-	3.7	Nat. Forest
Ci	4- 38	-	-	4- 38	-	4.7	Nat. Forest
Fdi	-	1- 45	-	1- 45	0	0	Private Land
Py	-	1- 20	-	1- 20	0	0	Private Land
Fdi	-	1- 8	-	1- 8	0	0	State Forest
Totals:	168-2255	16-230	-	184-2485			
Grand Total USA	181-2352	27-404.5	5-80	213-2836.5			
Grand Total Inland Mountain West (Canada & USA)	190	42	5	237			

[a] Classification — Stage
- Developing — site clearing or preparation and/or under propagation.
- Established — 80%+ planted.
- Producing — orchards that have produced greater than 40% of seed target in any one year.

List of Species Abbreviations

Fdc	Douglas-fir (coast)	Pseudotsuga menziesii (Mirb.)
Fdi	Douglas-fir (interior)	Franco var. menziesii
Lw	Western larch	Larix occidentalis Nutt.
Py	Ponderosa pine	Pinus ponderosa Laws.
Pw	Western white pine	Pinus monticola Dougl.
Pl	Lodgepole pine	Pinus contorta var. latifolia
Se	Engelmann spruce	Picea engelmannii (Parry) Engelm.
Sx	Interior spruce (commonly white x engelmann hybrids)	Picea sp.
Sw	White spruce	Picea glauca (Moench.) Voss
Bg	Grand fir	Abies grandis (Dougl.) Lindl.
Bsr	Shasta red fir	Abies magnifica var. shastatensis Lemm.
Bw	White fir	Abies concolor (Gorde & Glend.) Lindl.
Ps	Sugar pine	Pinus labertiana Dougl.
Ci	Incense cedar	Libocedrus decurrens Torr.

PRODUCTION OF IMPROVED WESTERN WHITE PINE AND DOUGLAS-FIR

AT POTLATCH CORPORATION'S CHERRYLANE SEED ORCHARD

Roger L. Blair

ιBSTRACT: Potlatch Corporation's tree improvement ›rogram includes grafted seed orchards for western ›hite pine and Douglas-fir. Production of improved ›eed at these facilities is discussed in light of :he attributes of the orchard site, cultural ›rocedures designed to promote early and consistent ›eed production, and supplemental mass pollination. :mplications of orchard planting design are dis-:ussed as they affect production of white pine seed ›ith varying degrees of rust resistance and Douglas-ir seed adapted to a range of elevational zones.

NTRODUCTION

otlatch Corporation's Western Division began its rtificial regeneration program in 1979. At that ime the first crop from the Lewiston seedling roduction facility was outplanted. Since then the egeneration program has grown to the production f 1.8 million seedlings per year sufficient to egenerate 4,000 acres with present planting pacings.

rior to beginning the artificial regeneration rogram, an extensive planning process indicated hat sufficient acres of Douglas-fir and rust-esistant white pine would be planted to justify ree improvement programs in these species. Based n an evaluation of programs elsewhere and existing esearch data, we decided to develop the grafted eed orchard of both species on a carefully chosen eed orchard site.

)CATION

ıe site on which the seed orchard is located is :itical to its long-term capabilities of high, ›nsistent cone production (Werner 1975). Ex-›rience in the Southeast and Pacific Coast as ›ll as in New Zealand has indicated that the ›llowing factors contribute to a good seed :chard location:

1. Warm, dry climate. Sweet (1975) summarizes regional differences in flowering by indicating that high annual flower production and reduced periodicity appear to be associated with hot, dry summers. Searching for sites with these characteristics has become a major factor in seed orchard siting in the Pacific Northwest. In addition to the promotion of abundant flowering, the frequency of flower-damaging late spring frosts is greatly reduced or even eliminated. Potlatch Corporation's Cherrylane site is located in the Clearwater River valley east of Lewiston, Idaho. Annual precipitation is about 30 cm with typically hot, dry summers. The growing season is substantially longer than that which occurs at the elevations where white pine is native.

2. Isolation from natural stands. Although this site is well within the latitudinal and longitudinal boundaries of the ranges of interior Douglas-fir and western white pine, the site is remote by several kilometers from natural occurrence of either species. This will greatly reduce the potential for pollen contamination from unimproved surrounding trees, a factor particularly important for western white pine where blister rust resistance is critical. In addition, cone and seed damaging insects should be much easier to control without an uncontrolled population in surrounding stands (see Haverty and Shea, this publication).

3. Fertile, well-drained soils. While the sites upon which cone production is best do not always support maximum vegetative growth, good fertility is required for successful orchard establishment and good early vegetative growth. The Cherrylane site is a sandy loam which had been farmed for many years prior to orchard establishment. Soil pH is about 5.5, satisfactory for conifer growth. The site is adjacent to the Clearwater River and is hence alluvial in nature. At a depth of one to two meters, the soil grades to nearly pure river sand. These soil characteristics allow the soil moisture regime to be maintained at nearly any desired level with the existing irrigation system. Nutrients can be added or withheld as needed.

LAYOUT

Since the orchard is located in a deep, narrow valley, wind currents are greatly influenced by

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ıper presented at the Conifer Tree Seed in the ıland Mountain West Symposium, Missoula, MT, ıgust 5-6, 1985.

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topography. Although large weather systems can cause unpredictable wind direction, the more usual air drainage pattern is downriver, east to west. The orchard has been laid out to utilize these wind patterns (see figure 1). For example, in establishing a small section of a Douglas-fir seedling seed orchard, a gradient was utilized from low elevation seed sources to high elevation from the northern boundary of the orchard to the southern boundary. Given that most pollination occurs among neighboring trees, one can reforest sites with differing elevations with seed collected from the appropriate area of the orchard.

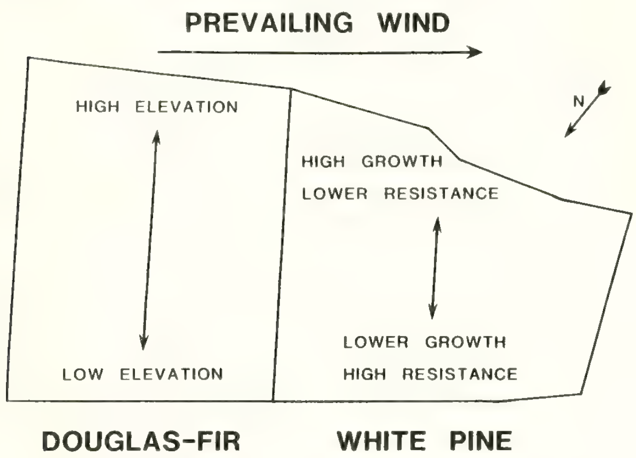

Figure 1.--Use of prevailing wind flow patterns in orchard design at Potlatch Corporation's Cherrylane Seed Orchard.

This layout procedure can be applied to other characteristics. For example, as data on rust resistance become available for our western white pine selections, a gradient from high resistance (with less emphasis on growth and form) to lower resistance (with more emphasis on growth and form) will be established across the seed orchard. This will be accomplished through the roguing process in the existing orchard and in the establishment of new orchard sections. Once again seed can be collected from the appropriate area in the orchard to match the requirement of the planting site. Sites known to be particularly high in rust hazard can be reforested with seed of maximum resistance. This procedure maximizes the utilization of expensive seed orchard sites (Blair 1983).

MANAGEMENT

Irrigation

Because of the orchard location and soil type, irrigation is essential for orchard establishment and maintenance. An irrigation system, utilizing overhead impact irrigation heads, was in place for the farming operation. This system was utilized during the first few years of orchard establishment and growth. This system soon became inadequate because of the labor-intensive nature of the movable pipe system, the interception of irrigation water by the developing crowns and the added cost of continued vegetation control with the broadcast irrigation.

The system has been replaced with a drip system designed to provide up to three gallons per hour per tree. With the orchard in full production, this system is sized to have the capacity to provide 18 gallons per tree per day. As the orchard is thinned and rogued, individual trees can be provided more water if needed.

An unforeseen problem with the drip system was t development of slime mold in the system and henc plugging of the emitters. Because water moves slowly through the drip irrigation pipes, incuba conditions for the slime mold organism were righ for rapid proliferation. This problem has been corrected by injection of chlorine in the final stages of an irrigation set.

Fertilization

Both broadcast and individual tree fertilization have been conducted during the early stages of orchard establishment and growth. These methods were utilized during the period when overhead irrigation was in place. Injection of liquid fertilizers is now being accomplished through th drip irrigation system. The present fertilizatio regime is designed to maximize vegetative growth and uses a complete fertilizer (12-8-4, NPK).

Fertilization has long been known to improve co production in western white pine (Barnes 1969). Timing and formulations of fertilizers and thei interaction with irrigation are not well understood particularly for site conditions similar to tho at the Cherrylane Orchard. Cooperative researc on this subject is planned for 1986.

Supplemental Mass Pollination

Seed cone production has been early and consist on many of the 60 clones in the white pine seed orchard. Seed cone counts conducted in the spring of 1985 showed that 44 of the 60 clones were flowering by four years after grafting. An average of nine seed cones per tree were produced.

A major, but not unexpected, problem has been pollen production. Only a few of the 60 clones have produced pollen in significant amounts. To offset this imbalance, supplemental mass pollination experimentation was begun this year. Pollen collected at the U.S. Forest Service white pine arboretum in Moscow, Idaho, in the spring of 19[illegible], was utilized. This pollen was collected from individuals known to be resistant to blister rust. An assembly used to inject a flux (powdered metal) into an air stream (a system used in gas welding) was modified to inject pollen. Commercially available high pressure nitrogen cylinders were utilized as a compressed air source. Air flow was directed at a seed cone cluster at 18 pounds per square inch. Although hampered by cool, wet weather, this device worked well mechanically and was exceptionally efficient in the use of pollen. Over 1400 flowers were pollinated, most two or three times, utilizing less than a pint of pollen.

Supplemental mass pollination offers the opportunity to control pollen source as well as to improve flower set and seeds per cone. This technology may be extremely important for western white pine where maximum blister rust resistance is required on many sites for successful plantation establishment.

SUMMARY

The Cherrylane Seed Orchard is believed to be ideally located for consistent high production of improved white pine and Douglas-fir seed. Although orchard establishment did not begin until 1979, preliminary indications are that early and consistent flower production will result. Orchard management is simplified by the location and soil conditions.

Orchard layout is designed to utilize prevailing airflow patterns to produce seed tailored for the site requirements. Supplemental mass pollination should speed our ability to produce seed in higher quantities and with desired characteristics.

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POTENTIAL AND ACTUAL SEED YIELDS FROM

A SOUTHERN PINE SEED ORCHARD

David L. Bramlett

ABSTRACT.--Monitoring the seed production on 26 sample trees in a loblolly pine (Pinus taeda L.) seed orchard in Georgia indicated that only 18.6 percent of the potential seed crop was recovered. Cone survival of the initial flower crop steadily decreased during the 18-month observation period, with an October 1978 cone efficiency of 0.585 of the original 1977 flower crop. Seed yields per cone were lower than expected for loblolly orchards and averaged only 50.4 filled seeds per cone and a seed efficiency of 0.375. Extraction efficiency and germination efficiency averaged 0.833 and 0.868, respectively. Seed yields from this orchard could be increased by increasing the size of the potential seed crop (flowers) or by increasing the overall seed orchard efficiency. Results indicate that a more intensive pest management program would reduce cone and seed losses and substantially increase seed orchard yields.

INTRODUCTION

To effectively and efficiently produce high levels of viable seed in southern pine orchards, managers need to have an accurate inventory of the annual seed production potential, and need to monitor the actual percentage of the seed crop that is harvested. An inventory-monitoring system (IMS) is currently being used in Federal, State, and industrial seed orchards (Bramlett and Godbee 1982). The system utilizes sample trees to quantify total flower production in the orchard and sample branches to periodically track the developing cone crop.

The use of IMS allows seed orchard managers to effectively allocate cone harvesting labor and equipment and to efficiently manage a pest control program on a cost-benefit basis. Effective and efficient management of seed orchards means that seed yields can be increased and that more genetically improved southern pine seedlings will be available for planting.

Paper presented at the Conifer Tree Seed in the Inland Mountain West Symposium, Missoula, MT, August 5-6, 1985.

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METHODS

Twenty-six loblolly pine (Pinus taeda L.) sample trees were selected in the Georgia Kraft Piedmont Seed Orchard, Greensboro, GA. Sample trees were randomly selected by row and column designations without prior visual inspection. The sample trees averaged 18 cm in diameter and 8.8 m tall. Tree ages ranged from 8 to 12 years old, with an average age of 10 years. In April 1977, approximately 2 weeks after female flower receptivity, the total flower count, including all healthy, damaged, or dead strobili, was tallied for each sample tree. At the time of the total flower count, eight sample branches were tagged and their initial flower count recorded as both healthy and dead flowers. The sample branches were distributed throughout the tree crown but were not randomly selected locations.

After the initial count, additional counts of all live flowers, conelets, or cones on the sample branches were completed in July and October of 1977 and in April, July, and October 1978. Mature cones were harvested from the whole tree in October of 1978 and classified as healthy, damaged, or dead. A cone analysis (Bramlett and others 1978) was completed on 10 random cones from each ramet. In the cone analysis the following properties of individual cones were observed: fertile scales, aborted ovules, total seed, filled seed, and germinated seed. Values of seed potential (SP), seed efficiency (SE), extraction efficiency (EE), and germination efficiency (GE), were calculated for each cone.

RESULTS

Flower and cone production data are presented in table 1. For the 26 sample trees, the total flower count ranged from 80 to 1,534, with a mean value of 444 flowers per tree. On the sample trees a total of 3,660 flowers were tagged for the periodic sample branch observations. The original flower count decreased with time from April 1977 to October 1978. Individual trees had varying survival rates ranging from 26.7 to 82 percent of the original flower count, with an overall average of 58.5 percent.

A similar observation of cone survival could be generated by comparing the total number of healthy cones harvested to the total number of flowers. For the 26 study trees an average of 63.4 percent of the flowers were harvested as mature cones. A regression (R^2 = 0.67) of the observations demonstrated a highly significant (P = .001) regression equation as follows:

Table 1.--Total flower count per sample tree and survival of flowers on branches from April 1977 through October 1978

Sample tree	Total flowers	Sample flowers	Survival year 1 Apr	July	Oct	Survival year 2 April	July	Oct
1	1,534	217	213	213	213	210	173	125
2	514	165	163	160	153	146	135	102
3	440	140	136	128	126	118	88	53
4	1,256	222	207	202	201	200	193	184
5	609	153	141	139	132	131	98	85
6	602	157	148	146	142	142	125	99
7	301	149	139	129	126	126	115	103
8	203	100	88	79	67	63	63	57
9	551	199	196	192	192	187	170	133
10	581	188	170	148	138	130	120	102
11	319	144	119	109	106	97	95	87
12	94	90	80	73	70	65	65	55
13	325	146	133	115	107	104	72	39
14	536	245	232	215	200	180	162	140
15	190	101	99	96	82	78	76	53
16	80	67	63	62	56	49	49	46
17	115	84	80	77	75	74	69	62
18	83	64	63	62	62	62	47	42
19	674	83	81	65	62	60	55	44
20	572	164	162	158	149	148	135	125
21	143	110	98	100	54	49	46	37
22	801	183	167	135	106	100	97	92
23	130	112	97	96	89	89	89	81
24	113	86	78	69	68	68	63	63
25	267	131	128	81	73	69	59	39
26	515	160	148	128	120	114	105	95
Sum	22,548	3,660	3,429	3,177	2,969	2,859	2,564	2,143
Mean	444	141	132	122	114	110	99	82

TREECE = 0.088 + 0.933 x OCT2CE

Where:

TREECE = total healthy cones (whole tree) divided by total flowers (whole tree)

OCT2CE = Total healthy cones (sample branches) divided by total flowers (sample branches)

more useful relationship for the orchard nager would be to predict the number of althy cones (PREDCONES) based on the served total tree flower count (TOTALFLO) d the sample branch cone survival for the ee (OCT2CE).

Thus: PREDCONE = TOTALFLO x OCT2CE

tual observations from the 26 sample trees dicated a very strong relationship between the tal cone production per tree (TOTCONE) and the lculated PREDCONE value. No statistically gnificant differences were present between e mean values of PREDCONE and TOTCONE for e 26 sample trees in this study. A very ghly significant relationship ($R^2 = 0.97$) n be described by the regression equation:

TOTCONE = 20.88 + 0.9612 x PREDCONE

Results of the cone analysis indicated that only an average of 50.35 filled seeds were produced per cone from the 260 sample cones (table 2). The seed efficiency calculated by the filled seeds per cone by the seed potential (Bramlett and others 1978) averaged 0.376 for the sample cones. Extraction efficiency calculated by dividing the number of extracted seeds by the total number of seeds per cone averaged 0.833. Germination efficiency was calculated as the number of filled seed per cone germinating in a laboratory test divided by the total number of filled seed per cone. The average observed value was 0.868.

With the four major components of seed orchard monitoring--CE, SE, EE, and GE--an overall seed orchard-to-nursery efficiency value (SO-NE) can be calculated as a product of the four parameters:

SO-NE = CE x SE x EE x GE

The average efficiency values for each tree are shown in table 3.

Table 2.--Cone analysis of 260 loblolly pine cones from Georgia Kraft Piedmont Seed Orchard, Greensboro, GA

Variable	Mean	Standard deviation
Cone length (mm)	82.13	13.08
Cone width (mm)	38.22	3.93
Fertile scales (no.)	66.00	10.47
First yr. aborted ovules (no.)	54.06	29.42
Second yr. aborted ovules (no.)	4.95	8.73
Extracted seed (no.)	64.33	38.03
Total seed (no.)	73.00	37.28
Filled seed (no.)	50.35	32.82
Empty seed	22.65	76.73
Germinated seed (no.)	46.92	32.89
Seed potential (no.)	132.01	20.95
Seed efficiency (SE)	0.376	0.23
Extraction efficiency (EE)	0.833	0.21
Germination efficiency (GE)	0.868	0.25

Table 3.--Values for cone efficiency (CE), seed efficiency (SE), extraction efficiency (EE), germination efficiency (GE), and seed orchard-to-nursery efficiency (SO-NE) for individual loblolly pine sample trees in the Georgia Kraft Piedmont Seed Orchard, Greensboro, GA

Sample tree	Efficiency value				
	CE	SE	EE	GE	SO-NE
1	0.576	0.728	0.984	0.997	0.411
2	0.618	0.684	0.972	0.973	0.400
3	0.379	0.583	0.933	0.906	0.187
4	0.829	0.425	0.985	0.988	0.343
5	0.556	0.485	0.968	0.979	0.255
6	0.631	0.490	0.901	0.858	0.239
7	0.691	0.399	0.963	0.995	0.264
8	0.570	0.599	0.957	0.958	0.313
9	0.668	0.378	0.816	0.982	0.203
10	0.543	0.338	0.763	0.912	0.127
11	0.604	0.234	0.826	0.779	0.091
12	0.611	0.100	0.478	0.915	0.027
13	0.267	0.177	0.780	0.947	0.034
14	0.571	0.173	0.807	0.949	0.076
15	0.525	0.060	0.520	0.212	0.003
16	0.687	0.042	0.519	0.496	0.007
17	0.738	0.329	0.932	0.969	0.219
18	0.656	0.412	0.639	0.950	0.164
19	0.530	0.480	0.754	0.785	0.151
20	0.762	0.715	0.938	0.934	0.478
21	0.336	0.290	0.924	0.909	0.082
22	0.503	0.328	0.878	0.905	0.131
23	0.723	0.226	0.891	0.386	0.056
24	0.733	0.537	0.916	0.989	0.357
25	0.298	0.262	0.695	0.929	0.050
26	0.594	0.291	0.909	1.000	0.157
Mean	0.585	0.376	0.833	0.869	0.186

ISCUSSION

mean CE of 0.585 indicates that only 58 ercent of the potential cone crop produced ealthy cones. Although the monitoring system oes not quantify specific causes of cone loss, bservations during the periodic counts are used o identify the types of cone loss. Insects are enerally the major cause of cone mortality, but ungal, environmental, and physiological causes re also known to cause mortality of loblolly pine lowers, conelets, or cones. The observed CE alue for the 1978 cone crop appears to be about verage for moderately protected loblolly pine eed orchards. Certainly the cone survival could e improved by increasing the degree of rotection in the orchard and a major gain in CE ould most likely occur from a more intense pest anagement program.

he average seed efficiency value of 0.376 is onsiderably below expected value for well-rotected seed orchards. In the 1978 cones, 2.5 percent of the potential ovules failed to evelop a filled seed. First-year aborted ovules ere the major type of seed losses, with an verage of 54.06 per cone. These losses could be rom insufficient pollen or from insect damage. f the two possible causes, insect damage by the eaffooted pine seedbug (Leptoglossus corculus Say) appears to be the most likely cause of ovule rtality (DeBarr and Ebel 1973). Once the vules enlarged in the second year of development, vule abortion continued at a lower rate (average .95 per ovule). After seedcoat formation and ertilization, embryo mortality produces an empty eed. Causes of empty seed include insect damage, ngi, embryonic lethal alleles, and perhaps nvironmental stress. The total number of empty eed per cone was 22.65 and account for 31.0 ercent of the total developed seed per cone. To ncrease seed efficiency, better insect control ould appear to be the highest priority. If nsects are adequately controlled, SE values ould approach 0.65 to 0.75.

e average extraction efficiency of 0.833 for e sample cones is lower than the 0.90+ nsidered normal for the species. Unfortunately boratory extraction may not accurately simulate erational orchard extraction. Thus the observed value for this orchard should be verified by tractions from the operational orchard tractory. Low EE values could be caused by rly harvesting of cones and improper opening and traction. For southern pines, seed tractories with recent innovations normally cover a high percentage of seeds from harvested nes.

rmination efficiency averaged 0.868 for the mple cones. This value is somewhat lower than rmal for loblolly pine. No apparent cause of e lower GE value was evident. Normal values are 90 to 0.95 for loblolly orchard seed.

The overall seed orchard-to-nursery efficiency of 0.186 indicates that only 18.6 percent of the potential seed crop was recovered as viable seed for the nursery. Conversely, 81.4 percent of the potential seed crop was lost to numerous destructive causes. Based on the monitoring values, seed production of the orchard could be increased by reducing losses and subsequently raising the SO-NE value. The most obvious change in management strategy would be to increase the intensity of insect protection. Several major insect pests can be controlled with an integrated pest management program (DeBarr 1981). Further monitoring would then be required to compare the effectiveness of the pest management program in terms of a higher SO-NE value. The other approach to increase the orchard seed yields would be to increase the total female flower production. Cultural practices including fertilization, subsoiling, and thinning could be used to stimulate increased flower production. Even planting more acres of orchard is an alternative. The most cost-effective procedure, however, would be to evaluate the current management program and to continue monitoring annual seed and cone crops to measure the effectiveness and efficiency of the seed orchard management program.

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EFFECT OF NITROGEN FERTILIZER AND

GIRDLING ON CONE AND SEED PRODUCTION OF WESTERN LARCH

Russell T. Graham

ABSTRACT: Western larch (Larix occidentalis Nutt.) is a poor cone and seed producer throughout northern Idaho. Because the species is important commercially, techniques for increasing seed production for both artificial and natural regeneration are needed. A study was conducted with western larch trees to evaluate the effectiveness of fertilizing, girdling, and a combination of fertilizing and girdling, as a means of increasing seed production. Girdling dominant and codominant 70-year-old western larch at the base of the live crown was very effective in stimulating cone production; the application of ammonium nitrate fertilizer in combination with girdling did not increase seed yield. Fertilizer alone did not increase cone production; rather, it appeared to decrease the number of seeds per cone. Cones from trees fertilized, girdled, and both fertilized and girdled had heavier seeds than cones produced by untreated trees.

INTRODUCTION

Western larch (Larix occidentalis Nutt.) is an infrequent and sporadic cone producer throughout northern Idaho. Since 1970, inventories of western larch seed for northern Idaho forests have been inadequate to meet needs of artificial regeneration programs. Because western larch is an important commercial tree species and the demand for seed exceeds the supply, a method of increasing seed production is needed.

Thinning forest stands has been shown to increase cone production in conifers. Wenger (1954) and Bilan (1960) showed that thinning increased cone production in loblolly pine (Pinus taeda L.), and Barnes (1969) found up to a fourfold increase in female strobilus production caused by thinning western white pine (Pinus monticola Dougl.). Barnes (1969) also found tree spacings of 9-m (29.5 ft) to be more effective than 6-m (19.7-ft) spacings for stimulating production of female strobili.

Mineral nutrition may also directly influen cone production of conifers. Nitrogen appe to be the most important element in cone production. Coast Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco.) (Ebell 1962, 197 western white pine (Barnes 1969), and Rocky Mountain ponderosa pine (Pinus ponderosa va scopulorum Engelm.) (Heidmann 1984) increas cone production in response to applications nitrogen fertilizer. In addition, the type timing of fertilizer application can be ver important for cone initiation. Ebell (1972 found calcium nitrate fertilizer superior t urea and ammonium sulfate fertilizers in stimulating Douglas-fir cone production. H also found that application of fertilizer a 5 percent of the vegetative buds had burst May stimulated cone production better than spring or late spring applications. Fertilization rates of 225 kg per ha (201 l acre) of nitrogen to 1 800 kg per ha (1,607 per acre) of nitrogen have been found effec in increasing cone production of conifers.

Girdling is an effective method of increasi cone yields in some conifers. Bilan (1960) showed an increase in cone production attributable to girdling loblolly pine. Al Ebell (1971) found a 300 percent to 400 per increase in the number of cones on stems of Douglas-fir girdled at breast height compar untreated stems. Holst (1959) reported a twentyfold increase in the number of cones produced on red pine (Pinus resinosa Ait.) because of girdling. He also found girdlin trees at the base of the live crown was fou times as effective as girdling at breast he for stimulating cone initiation. Stephens (1964) girdled individual branches of easte white pine (Pinus strobus L.) and found 300 percent more female cones on the girdle branches than on the untreated branches.

Most girdles to stimulate cone production o conifers have been overlapping cuts up to o internode apart severing the phloem on two of the trunk or branch. They range from si saw cuts to complete removal of the bark. Girdling at breast height by removing a 2.5 (1-inch) strip of bark slightly more than h the stem circumference with an overlapping on the opposite side, one internode above t first, was used successfully by Ebell (1971 increase the number of cones on Douglas-fir

The purpose of this study was to examine th effects of girdling and fertilization,

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individually and combined, as a means of increasing seed production of western larch. Reported here are the results of such a combination of treatments on cone and seed production in a young western larch stand in northern Idaho.

METHODS

In 1980, we selected for this study a 70-year-old stand of western larch located on the Wallace Ranger District, Idaho Panhandle National Forests, 8 km (5 mi) east of Mullan, ID, near the Idaho-Montana border. The stand was thinned to a residual basal area of 9.2 to 13.8 m^2 per ha (40 to 60 ft^2 per acre). Logging slash was machine piled and burned in the spring and early fall of 1981.

Because snow cover prevented applying fertilizer in the spring before bud burst, the study was established in the fall of 1981. The treatments could then influence bud formation during the 1982 growing season. Seventy-two dominant and codominant trees were chosen in the stand and divided into six-tree groups. Only the best formed and more vigorous trees were chosen for inclusion in the study. Three treatments were randomly applied to six-tree groups in three replicates. The treatments included:

1. Fertilize: 336 kg per ha (300 lb per acre) of N in the form of ammonium nitrate was broadcast with a hand spreader under the crown of each tree, all within the drip line. This resulted in fertilizing a 4.5-m (14.8-ft) radius around the base of each tree.

2. Girdle: The trees chosen for girdling were climbed (using climbing spurs) to the base of the live crown. Here, a hand pruning saw was used to sever the phloem for one-half the circumference. A similar cut was made on the opposite side at least the length of the circumference down the tree. This resulted in overlapping cuts.

3. Girdle and fertilize: Trees were girdled and fertilized using the same procedures as for treatments 1 and 2.

Eighteen trees were maintained as controls, with no treatment. The treatment strategy resulted in a randomized complete block experiment with subsampling (table 1).

In the fall of 1983 each tree producing cones was climbed, and the cones were collected. Seeds were extracted from the cones and cleaned at the Coeur d'Alene Nursery at Coeur d'Alene, ID. Cones per tree, sound seeds per cone, and mean seed weight were recorded. In addition, a germination trial was conducted on the seed with [illegible], 14, and 28 days of stratification. An analysis of variance for a randomized complete block design was used to analyze the data (table 1). Duncan's multiple range test was used to detect differences among the treatment means.

Table 1.--Analysis of variance table for a study of effects of girdling and fertilization on cone and seed production of western larch in northern Idaho

	Analysis of variance	
Source	Degrees of freedom	Expected mean squares
3 Treatments and control	3	$\sigma^2 + 6\sigma^2_\varepsilon + 18\sum\tau^2_i/3$
3 Blocks	2	$\sigma^2 + 6\sigma^2_\varepsilon + 24\sum\beta^2_i/2$
Experimental error	6	$\sigma^2 + 6\sigma^2_\varepsilon$
Sampling error	60	σ^2
Total	71	

RESULTS

Girdling was highly successful in stimulating cone production on western larch. Trees that were only girdled had a mean of 832 cones per tree, the untreated trees had a mean of 77 cones per tree, the fertilized trees had a mean of 87 cones per tree, and the girdled and fertilized trees had a mean of 16 cones per tree (fig. 1). There were no significant ($P \leq 0.05$) differences in mean cones per tree among the fertilized, control, and the combination treatments, but the mean for the girdled treatment was significantly higher than the other means. Saw cuts on the girdled trees healed over within 1 year.

The only treatment that influenced the number of seeds per cone was fertilization. This treatment appeared to decrease the number of seeds per cone with a mean of only 0.63 (fig. 2); the control and other treatments all produced from 7 to 8 seeds per cone. The mean number of seeds per cone for the fertilized treatment was significantly lower than the means for the other treatments.

The treatments applied to stimulate cone production also affected seed weight. Seeds produced on the control trees were significantly lighter (3.11 mg) than seeds produced on treated trees (fig. 3). The heaviest seeds were produced on trees fertilized only, with a mean seed weight of 4.59 mg.

Other tree and site variables were tested to see if they had a significant relationship to cone production. Tree height, diameter at breast height (d.b.h.), crown ratio, crown density, and surrounding basal area were all tested to see if they were significantly related to cone production in addition to the treatments. The only variable close to being significant was crown ratio at the 0.163 level (table 2).

Tree height, crown density, d.b.h., and residual basal area were all nonsignificant in explaining the variation of cone production in western larch. In addition, there were few significant differences found among the treatments for the tree and stand characteristics (table 2). There were no differences in germination among the treatments after stratification of 0, 14, or 28 days. Germination means were 12, 95, and 96 percent, respectively, for the different stratification periods.

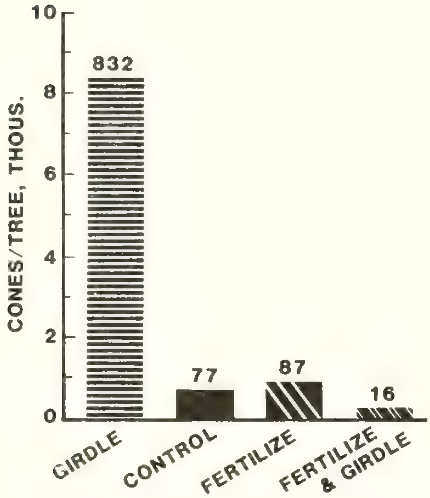

Figure 1.--Mean cones per tree produced by western larch after girdling, fertilization, and both treatments and by controls. The mean for cones after girdling was significantly higher than control and other treatment means. Differences among treatment means were not significant ($P \leq 0.05$).

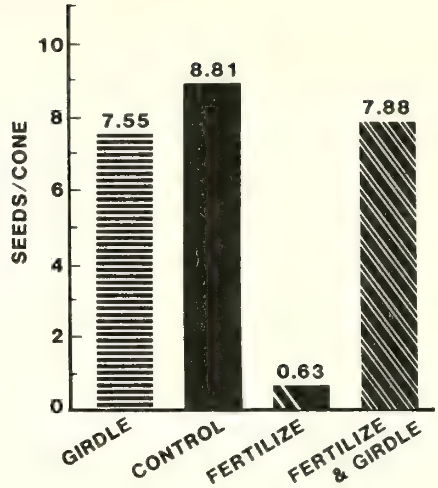

Figure 2.--Mean numbers of seeds per cone from western larch after girdling, fertilization, and both treatments and from controls. Fertilization apparently decreased the seed mean significantly. Other differences among means were not significant ($P \leq 0.05$).

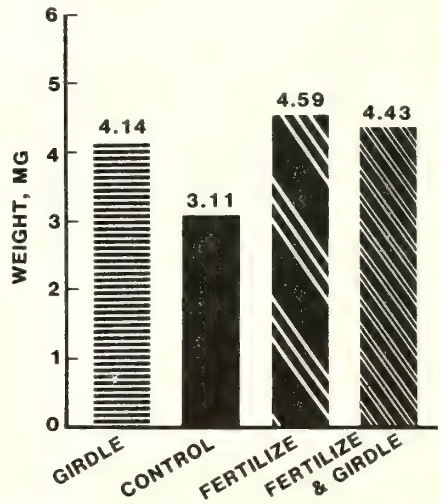

Figure 3.--Mean weights of seed produced by western larch after girdling, fertilization, and both treatments and by controls. The difference between the control mean and other means was significant ($P \leq 0.05$).

Table 2.--Mean tree and stand characteristics for western larch in northern Idaho by treatment and their significance in explaining cone production

Treatment	d.b.h.	Height	Crown ratio	Residual basal area	Crown density
	cm	m	percent	m^2/ha	
Control	[1]34.0a	28.9ab	31.7ab	8.66a	Good
Fertilize	35.3a	29.6a	35.0a	8.43a	Good
Girdle	33.5a	27.5bc	31.7ab	7.90a	Good
Fertilize and girdle	32.8a	27.0c	29.4b	6.89a	Good
Significance	.752	.367	.163	.752	.583

[1]Different letters indicate significant ($P \leq 0.05$) differences among treatments.

ISCUSSION

irdling of western larch to increase cone roduction appears to be an effective method for se in seed production areas and for natural egeneration. Trees that were girdled produced ore cones than trees that were fertilized only r both fertilized and girdled. Number of seeds er cone and mean seed weight appeared naffected by girdling, and girdle cuts were ealed within 1 year.

ne application of 336 kg of N per ha (300 lb er acre) in the form of ammonium nitrate seemed o offset the stimulus to cone production caused y tree girdling. The addition of nitrogen may ave increased tree vigor to the point that new rowth consumed the increased nutrients but luted any changes in hormones that may have ccurred. The addition of nitrogen appeared to nfluence seed weight, but not to a greater ktent than girdling alone.

e sawcuts apparently disrupted the anslocation of organic solutes in the phloem ough to stimulate cone production. When the wnward movement of organic solutes is blocked, ey tend to diffuse into the xylem and are anslocated back to the leaves and shoots of e crown (Kramer and Kozlowski 1979). These lutes containing carbohydrates, auxins, bberlins, and other compounds can concentrate leaves for fruit and seed production.

e accumulation of carbohydrates in the crown y not be directly associated with seed and ne formation. Ebell (1971) did not find an crease in the level of carbohydrates in the owns of Douglas-fir that had been successfully rdled to increase cone production. He ncluded that there was a doubtful relationship tween carbohydrates and reproductive bud rvival.

sides disrupting translocation in the phloem, her physical conditions within a tree may be tered by girdling. These include increased sture stress in tree crowns and changes in her physiological and nutritional processes at may increase cone and seed yields. In dition, the wound caused by a girdle may oduce wound response compounds that could be directed toward the crown to influence cone oduction.

dling trees at the base of the live crown pears very effective in stimulating cone oduction. The redirected movement of bohydrates and hormones caused by girdling be less diluted with girdles near the crown n with girdles at or near breast height. If re is a beneficial chemical response to the dling wounds, this would also be near the e-producing area of the tree.

rlapping cuts through the bark at the base of live crown created by a handsaw increased number of cones produced on open grown tern larch trees. Sawcuts healed after ear, making it possible to re-treat the trees relatively quickly with minimal permanent damage. However, climbing trees is time-consuming, and therefore expensive, and spurs often cause extensive damage. Therefore, with such good success by girdling at breast height in other species and the excellent results of this study, girdling at breast height should also be considered. Girdling trees at breast height may require more extensive bark removal to sufficiently disrupt translocation in the phloem. Heavier applications of fertilizer, in the range of 1,000 to 2,500 kg per ha (893 to 2,232 lb per acre) of N, might also be effective in stimulating cone production and should be investigated.

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FLOWERING OF PINACEAE FAMILY CONIFERS WITH GIBBERELLIN $A_{4/7}$ MIXTURE: HOW TO ACCOMPLISH IT, MECHANISMS AND INTEGRATION WITH EARLY PROGENY TESTING

Richard P. Pharis and Stephen D. Ross

ABSTRACT: Factors influencing the successful use of $GA_{4/7}$ to promote early and enhanced flowering in Pinaceae family conifers are reviewed, including the mode and timing of application, together with interactions with other growth regulators and cultural practices. Prospects for evaluating the inherent growth potential of progeny at a very young age under phytotron conditions and integration with indoor-potted breeding orchards to accelerate the tree-breeding process are discussed.

INTRODUCTION

It has been known since the late 1950s that juvenility could be terminated (albeit temporarily) and precocious flowering induced at will in seedling members of many Cupressaceae and Taxodiaceae family conifers through the exogenous application of gibberellins (GAs) (see ref. in Pharis and Kuo 1977). The potential usefulness of this treatment for accelerating the excruciatingly slow processes of breeding and production of genetically improved tree seeds was, of course, immediately recognized. It appeared for many years, however, that this effectiveness of GAs for promoting earlier and enhanced flowering in the Cupressaceae and Taxodiaceae did not extend to Pinaceae family conifers, which includes most of the commercially important species for which tree improvement programs were under way.

Then, in 1973, we discovered with Pseudotsuga menziesii (Mirb.) Franco (Pharis 1976; Ross and Pharis 1973) and later with other species (references cited in: Pharis and King 1985; Pharis and Kuo 1977; Pharis and Ross 1984; Ross and others 1983; table 1); that the GA in common use, GA_3, was the wrong one for using with the Pinaceae. Whereas GA_3 was especially effective with conifers of the Cupressaceae and Taxodiaceae, Pinaceae family conifers were found to exhibit a specificity for certain GAs less polar than GA_3, most notably a mixture of GA_4 and GA_7 ($GA_{4/7}$) (Pharis and Ross 1984; Ross and others 1983; table 1). In the past decade over 80 research reports have noted a positive flowering response to $GA_{4/7}$ for at least 18 Pinaceae species representing 5 of the 6 genera of this important family (table 1). The genus Abies is not included in this list but it has only been represented by a single study with A. homolepsis which gave equivocal results (Katsuta 1981).

The successful promotion of flowering is not, however, just simply a matter of spraying trees with $GA_{4/7}$. For reasons not yet understood (Pharis and Ross 1986) conifers of the Pinaceae are not nearly as responsive to applied GAs ($GA_{4/7}$) as are those of the Cupressaceae and Taxodiaceae (to GA_3). In this paper we will consider those factors and conditions which if met should ensure the successful promotion of early and enhanced flowering in Pinaceae family conifers using $GA_{4/7}$.

FACTORS INFLUENCING $GA_{4/7}$ EFFICACY

Treatment Timing

As with other stimulation treatments, $GA_{4/7}$ is only effective if its application brackets the period of cone-bud differentiation for the species in question. Owens gives elsewhere in this proceedings the times when seed- and pollen-cone buds first become anatomically distinct from vegetative buds for a number of North American conifers. He notes, however, that these times are the latest that treatments could be expected to promote flowering. For maximum effectiveness the treatment should be applied 2 to 3 weeks earlier to influence the biochemical processes leading to anatomical differentiation of bud types.

A few words of caution regarding treatment timing are in order. Many workers make the mistake of relating treatments to calendar date rather than to stage of bud development. Depending on the year, genotype, site and associated environmental/cultural conditions, etc., bud phenology may vary by 2, 4 or more weeks in any given trial. Consequently, where $GA_{4/7}$ applications are timed to calendar date the treatment may be either too early or too late to influence cone bud differentiation (Ross 1985). Fortunately, it is not

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Table 1.--A checklist for species of Pinaceae family conifers that will flower in response to applicati of a mixture of the plant hormones, gibberellin $A_{4/7}$, with appropriate reference citations

Species	References
Larix leptolepis	(see ref. cited in Pharis and Ross 1984; Bonnet-Masimbert 1982)
L. decidua	(see ref. cited in Pharis and Ross 1984; Bonnet-Masimbert 1982)
Picea abies	(see ref. cited in Pharis and Kuo 1977; Pharis and Ross 1984; see also Chalupka and Giertych 1977; Dunberg 1979; Dunberg and Oden 1983b)
P. engelmannii	(Ross 1985)
P. glauca	(Cecich 1985; Marquard and Hanover 1984a; Marquard and Hanover 1984b; Pharis and Kuo 1977; Pharis and others 1985)
P. mariana	(Hall 1984)
P. sitchensis	(see ref. cited in Pharis and Ross 1984; see also Philipson 1981; Philipson 1983; Philipson 1985; Tompsett 1977)
Pinus banksiana	(see ref. cited in Pharis and Ross 1984; see also Cecich 1982; Cecich 1983)
P. caribaea	(Harrison 1985)
P. contorta	(see ref. cited in Pharis and Kuo 1977; Pharis and Ross 1984)
P. densiflora	(see ref. cited in Pharis and Kuo 1977; Pharis and Ross 1984; Katsuta 1981)
P. elliottii	(see ref. cited in Pharis and Kuo 1977; Pharis and Ross 1984 and see also Hare 1984)
P. palustris	(see ref. cited in Pharis and Ross 1984 and see also Hare 1984)
P. radiata	(see ref. cited in Pharis and Kuo 1977; Pharis and Ross 1984 and see also Ross and others 1984)
P. sylvestris	(see ref. cited in Pharis and Ross 1984 and see also Chalupka 1978; Chalupka 1984)
P. taeda	(see ref. cited in Pharis and Ross 1984 and also Hare 1984)
P. thunbergii	(see ref. cited in Pharis and Kuo 1977; Pharis and Ross 1984)
Pseudotsuga menziesii	(see ref. cited in Pharis and Kuo 1977; Pharis and Ross 1984; Pharis and Ross 1976; Pharis and others 1980; see also Owens and others 1985; Pharis 1976; Pharis 1978; Ross 1976; Ross 1977; Ross 1978; Ross 1979a; Ross 1979b; Ross 197 Ross 1983; Ross and Pharis 1973; Ross and others 1983; Ross and others 1985; Webber 1984; Webber and others 1985)
	(see ref. cited in Pharis and Ross 1984; see also Pollard and Portlock 1984)
Tsuga heterophylla Useful Reviews	(Dunberg and Oden 1983; Pharis 1978; Pharis and King 1985; Pharis and Kuo 1977; Pharis and others 1980; Pharis and Ross 1984; Pharis and Ross 1986; Ross and Pharis 1982; Ross and Pharis 1986; Ross and others 1983; Zeevaart 1983; Zimmerman and others 1985)

necessary to go through the laborious process of dissecting axillary buds and potentially reproductive terminal buds (in some species) to determine when they are at the proper developmental stage for treatment. Reproductive bud development is closely related to the seasonal pattern of shoot elongation (Owens, this proceedings).

For Pseudotsuga (Ross 1983) and Tsuga (Ross and others 1980) $GA_{4/7}$ treatment would begin in spring at about the time of vegetative bud burst, whereas for Picea (Marquard and Hanover 1984b) it should be delayed until the new shoot is about 75-85 percent elongated. For these and most other Pinaceae family conifers the difference in timing of seed- and pollen-cone buds is generally too small to be able to use treatment timing to influence conebud sexuality (Owens, this proceedings). However, this is not the case for some species of Pinus, where it is possible to preferentially promote either male or female flowering through, respectively, early and late applications of $GA_{4/7}$ (Chalupka 1984). Another point to consider is that all buds on a tree do not develop at the same rate; in larger tree there will be much greater variation in bud development associated with crown position. Thus, whereas 2 weeks or less of $GA_{4/7}$ application may suffice to sexually differentiate a given bud (Owens, this proceedings), a longer treatment time is required to bracket the differentiation for different buds throughout t entire tree crown. The duration of treatment will also depend on the population of trees bei treated and the magnitude of differences in the bud phenology. For most seed orchard populatio it appears that 4 to 6 weeks of $GA_{4/7}$ applicati is about optimal for P. menziesii.

Mode of Application

Gibberellin $A_{4/7}$ costs about \$13 to \$20 (Can.) per gram, depending on source, so it is importa that the mode of application be both effective and conserving of the hormone, as well as pract cal for operational use. The best mode of appl cation will depend on the species, the size of the trees being treated and whether the objecti

is to promote early and enhanced flowering for breeding purposes or for volume seed production. Thus, topical applications of $GA_{4/7}$ by micro pipette may be highly cost effective for the former but not the latter.

Foliar sprays are perhaps the most convenient method for applying $GA_{4/7}$ to large seed orchard trees. And, aqueous sprays containing an appropriate cationic surfactant have proved to be highly effective for certain conifers such as Tsuga heterophylla (Raf.) Sarg. (Ross and others 1980). However, for other conifers, including Pseudotsuga menziesii (Pharis and Ross 1976) and Larix species (Bonnet-Masimbert 1982), such foliar-applied $GA_{4/7}$ seems to be only poorly absorbed. Another problem with conventional foliar sprays is that they are quite wasteful of the $GA_{4/7}$. Ultra low volume (ULV) sprayers combined with anti-evaporant spray oils, which also facilitate foliar absorption, may provide a partial solution to both problems. Bower and Ross (1986) provide preliminary results which demonstrate its potential effectiveness for the operational $GA_{4/7}$ treatment of P. menziesii seed orchards. In this particular study, ULV spray applications in 2-percent spray oil elicited nearly three times the female flowering response at only 1/8 the dosage of $GA_{4/7}$ as the conventional aqueous surfactant formulation applied by high-volume mist sprayer.

Still for many conifers stem injection remains the most effective method for applying GAs (Pharis and Ross 1976; Bonnet-Masimbert 1982). As originally developed for Pseudotsuga menziesii, this involved feeding an aqueous solution of 25 to 100 mg $L^{-1} GA_{4/7}$ from a modified medical intravenous unit into a small (5/16-inch) hole drilled into the stem at the base of the live crown. Despite its effectiveness, the method was laborious -- injection holes plugged up after about 2 weeks and had to be redrilled -- and really only practical for treating relatively small trees. Philipson (1985) however, recently described a simpler method of stem injection which he found to be both quite convenient and highly effective for promoting flowering in large (6-m tall) Picea sitchensis (Bong.) Carr. trees. It involved drilling two shallow holes on opposite sides of the stem and then injecting with a syringe a concentrated ethanolic solution of $GA_{4/7}$. New holes were drilled after 2 weeks and the treatment repeated. Ross and Bower (1985, unpublished) are presently evaluating this quick method of stem injection (about 2 min/tree) on 4- to 14-cm diameter P. menziesii grafted propagules.

Interactions with Other Regulators

The less polar GAs are the only growth regulators that consistently promote flowering in Pinaceae family conifers (Pharis and King 1985; Pharis and Ross 1984; Pharis and Ross 1986; Ross and Pharis 1986).

The auxin, napthaleneacetic acid (NAA), was found by Hashizume (1967) to be an effective promoter by itself of female flowering in girdled Larix leptolepis saplings, but this was not the case for P. menziesii (Ross, unpublished results) or two species of Picea (Tompsett 1977; Dunberg and others, unpublished results). However, for these latter species NAA and other synthetic auxins were found to enhance the efficacy of applied GAs. In the case of sexually mature grafts of Picea sitchensis (Thompsett 1977) and in immature P. menziesii seedlings where the auxin was used at a higher concentration (Pharis and others 1980) the effect of applying NAA in conjunction with GAs was to promote male flowering at the expense of female flowering. However, with younger seedlings (table 2) and grafts (Ross 1976) of P. menziesii, synthetic auxins also enhanced the female flowering response to applied $GA_{4/7}$ although not to the same extent as for male flowering.

Table 2.--Female and male flowering responses by potted Pseudotsuga menziesii trees to stem injections of gibberellin $A_{4/7}$ ($GA_{4/7}$) alone and with the synthetic auxins, napthaleneacetic acid (NAA) or 2,4,5-triphenoxypropionic acid (2, 4,5-TP) (Ross, unpublished results, 1979)[1,2]

Treatment	Cone buds/tree (no. ± s.e.) Female	Male
Untreated	12 ± 6	24 ± 14
$GA_{4/7}$ alone	67 ± 15	50 ± 17
$GA_{4/7}$ + NAA	78 ± 14	133 ± 45
$GA_{4/7}$ + 2,4,5-TP	100 ± 18	138 ± 38

[1]Plants were 5-year-old rooted cuttings of physiological age 12-14 years at time of treatment; 20 plants/treatment and grown outdoors in 17 L containers.

[2]Growth regulators were infused into the main stem, $GA_{4/7}$ at 100 mg L^{-1} and each auxin at 5 mg L^{-1} in 0.02 percent ethanol:water, for 12 weeks commencing approximately 2 weeks prior to vegetative bud burst.

On the other hand, studies with Tsuga heterophylla (Ross and others, unpublished results) and Pinus radiata D. Don (G. B. Sweet, personal communications) have found no response to NAA, either by itself or with $GA_{4/7}$ or GA_3. It seems that further research is required to establish if auxins and possible other growth regulators interact with GAs to influence cone-bud sexuality in conifers as is clearly the case for many angiospermous plants (Pharis and King 1985).

Interactions with Cultural Treatments in the Field

Promotion of flowering under field conditions is a tricky business, especially where young trees are involved. No single treatment, including $GA_{4/7}$ should be expected to work if site and climatic factors are otherwise unfavorable for flowering, as frequently appears to be the case in many of our seed orchards. However, many studies have shown that the probability of success is greatest where $GA_{4/7}$ is applied in conjunction with a cultural treatment (for example, nondestructive stem girdling, nitrate fertilization, rootpruning, or drought) that by itself is often ineffective in promoting flowering.

Table 3.--Interaction between gibberellins $A_{4/7}$+ A_3 and stem girdling on flowering in 7-year-old Pseudotsuga menziesii grafts at the Weyerhaeuser Company, Rochester, WA, seed orchard (Cade and others, unpublished results, 1975)[1]

Treatment	Clones Producing		Cone buds/tree	
	Females (percent)	Males (percent)	Seed (no.)	Pollen (no.)
Untreated	24 a	26 a	2.2 a	62 a
Girdled only	35 a	40 b	1.7 a	27 a
$GA_{4/7}$ + GA_3 only	67 b	30 a	7.8 b	20 a
$GA_{4/7}$ + GA_3 + gird.	97 c	74 b	50.7 c	337 b

[1]Values followed by the same letter do not differ significantly at $P \leq 0.05$ based on Chi square (percentages) and Duncan's multiple range tests.

[2]Trees received double overlapping, half-circumferential band girdles, 6 mm wide and 130 mm apart, at onset of vegetative bud swelling.

[3]Stem injections of a 1:1 (w/w) mixture of $GA_{4/7}$ and GA_3 in 0.02 percent ethanol:water also commenced then and continued for 9 weeks, during which time each tree received on average 1.13 g of the GA mixture.

[4]Each treatment was tested on 1-7 (3.8 avg.) ramets from each of 56 sexually mature parent tree clones.

Table 3 provides a classic example of such synergism, in this case between stem injections of $GA_{4/7}$ + GA_3 and overlapping band girdles in a 7-year-old grafted P. menziesii seed orchard in western Washington. Wheeler and others (1985) have shown that the same girdling treatment can be highly effective in the promotion of flowering for similar aged grafts in another orchard in southern Oregon. However, the Washington orchard was located on a relatively cool, moist site that was generally not favorable for early flowering, and here stem girdling by itself was totally ineffective in increasing the production of seed or pollen-cone buds. The grafts responded with small (though significant) increase in female flowering from stem injections of $GA_{4/7}$ + GA_3 alone. Yet, when combined, the hormone and girdling treatments had a highly synergistic effect, increasing the mean production of seed- and pollen-cone cones relative to the otherwise best treatment by factors of 5.6 and 44, respectively. Ross and others (1980) report a similar synergism between $GA_{4/7}$ and calcium nitrate fertilization for field-grown rooted cuttings of mature Tsuga heterophylla clones.

It should not be concluded from the above that $GA_{4/7}$ is always the most effective treatment. There are examples for P. menziesii where girdling (Bower and Ross 1986) and root-pruning (Ross and others 1985) were each more effective in promoting flowering than $GA_{4/7}$ alone. However the point we wish to make is that best results have always been attained where the cultural treatment was applied in conjunction with the $GA_{4/7}$. What is furthermore important is that the magnitude of the synergism tends to be proportionately stronger for those inherently recalcitrant clones and families that without treatment might not contribute to seed production (Ross and others 1980; Ross and others 1985).

Benefits of Container Culture

The fact remains that, even with the best treatments, flowering under field conditions will still be subject to the vagaries of climate. Ross and others discuss elsewhere in this proceedings the practical advantages of managing small trees indoors in pots for seed production, central among which is the ability to provide optimal environmental conditions at the proper time for influencing cone-bud differentiation.

With P. menziesii, simply restricting the root volume of trees in small pots can by itself be sufficient to cause precocious or enhanced flowering. In one experiment grafts were either outplanted into the seed orchard in the spring of their second growing season or left outdoors in 2.1 L containers where they were kept well watered, with and without stem injections of 25 mg L^{-1} $GA_{4/7}$ for 6 weeks commencing at vegetative bud burst. The following spring only 14 percent of the outplanted grafts, but 80 percent of the potted but otherwise untreated grafts, initiated seed-cone buds, an average of 1.1 and 10.1 each, respectively. Treatment with $GA_{4/7}$ nearly trebled the production of seed-cone buds (to 28.1) by potted grafts and resulted in 94 percent of the grafts flowering.

A second experiment with 2-year-old rooted cuttings of P. menziesii seedlings only 2 years of age at time of propagation illustrates the importance of container size on flowering. Trees were repotted from 2.1 L into 6.3 , 19.7 or 76 L containers in early spring and received stem injections of $GA_{4/7}$ as above plus a heavy dosage of calcium nitrate. All trees were well watered and the following spring those in the smallest containers produced an average of 14.8 seed-cone buds each, compared to only 3.0 and 0.8 for trees in the 19.7 and 76 L containers, respectively.

Table 4.--Interaction between gibberellin $A_{4/7}$ ($GA_{4/7}$), water stress (WS) and stem girdling on female flowering in young potted Pseudotsuga menziesii trees (Ross, unpublished results, 1976)[1,2,3]

Treatment	Plants flowering (percent)	Seed-cone buds/tree (no.)
Untreated	5^a	0.1^a
$GA_{4/7}$ alone	50^b	6.5^b
$GA_{4/7}$ + WS[4]	60^b	19.1^c
$GA_{4/7}$ + gird.[5]	55^b	13.5^c
$GA_{4/7}$ + WS[4]+ gird.[5]	65^b	7.0^b

[1]Plants were 2-year-old rooted cuttings of physiological age 4 years from seed at time of treatment: 20 plants/treatment.

[2]Values followed by the same letter do not differ significantly at $P \leq 0.05$ based on Chi-square (percentages) and Duncan's multiple range tests.

[3]Stem injections of $GA_{4/7}$ at 25 mg L^{-1} in 0.05 percent ethanol:water began on 21 April and lasted 12 weeks.

[4]Throughout the period of GA treatment water stressed plants were allowed to attain an average pre-sunrise shoot water potential of -1.5 Mpa before watering to saturation. Non-stressed plants were well watered.

[5]Girdled plants received double overlapping, half-circumferential band girdles, 4 mm wide and 20 mm apart, beneath the lowermost live branch on 20 April.

It is not clear to what extent this reflects a more rapid build-up of favorable (to flowering) internal water deficits in the small containers, or reduction in root activity associated with pot binding (Bonnet-Masimbert 1982; Philipson 1983). Various studies on several conifers (table 4; Ross 1978; Brix and Portlock 1982; Bonnet-Masimbert 1982; Philipson 1983) have shown that drought produced by withholding irrigation frequently enhances synergistically the flowering response to applied $GA_{4/7}$ in potted trees. Note in table 4 that non-destructive stem girdling was nearly as effective in this regard as was drought, whereas the two cultural treatments applied together were apparently overly stressful and antagonized the flowering response to $GA_{4/7}$.

CONCLUSIONS

With Regard to Flowering

It appears to us, based on the plethora of successful reports noted in table 1 and in Pharis and Ross (1984), and the examples given in tables 2-4, that virtually any Pinaceae family conifer will be amenable to manipulation of early and/or enhanced flowering by the use of $GA_{4/7}$ + an appropriate cultural treatment. Additional gains in male flowering and increased female flowering may also be made through the judicious use of the auxin, NAA, given with the $GA_{4/7}$ and cultural treatment.

New species, and new or unusual climatic conditions (for field seed orchards) may require some additional empirical research with regard to optimal timing of treatment, dosages of hormone(s), and the most appropriate cultural treatment to use. In some locations climatic conditions (for example, wet cool, low solar insolation) may preclude successful field cone induction most years. In those cases, and perhaps in most instances, we recommend the use of potted propagules and heated plastic house environments during treatment (see paper by Ross and others, this proceedings).

In essence, there is now no excuse for a conifer tree breeder to wait for nature to bring on the 'natural' flowering that results from termination of the so-called 'juvenile phase'. All conifer species should be manipulable, even at very early ages, through the properly timed use of $GA_{4/7}$ application combined with an appropriate cultural treatment.

Additionally, enhanced production of seed from genetically superior propagules/F1 seedlings is now within our grasp (see Ross and others, this proceedings), and we believe that such an approach is, or can be, more cost effective than field seed orchards.

With Regard to Early Progeny Testing

Finally, we now have before us the very real possibility that inherently superior families, or even genotypes, can be tested at an early age (see table 5), and that young seedlings/germinants from these superior families and/or genotypes, can be multiplied clonally for outplanting. It is not unrealistic to visualize potted propagule seed orchards yielding, each

Table 5.--Effect of family and application of gibberellin $A_{4/7}$ mixture on the growth of *Pinus radiata* seedlings at different ages in the phytotron compared to growth rating of same families at age 9+ years in the field[a]

		Stem volume (cm^3) at ages[d] from germination			
		138 days[e]	175 days[f]		
Family code[b]	Growth rating at age 9+ years in field[c]	Control (no $GA_{4/7}$)	Control (no $GA_{4/7}$)	$GA_{4/7}$-treated[g]	Stem volume increase due to $GA_{4/7}$ treatment (%)
R4	Fast	14.7(1)[h]	37.4(2)[h]	53.5(1)	43
R3	Fast	13.1(2)	36.2(3)	41.9(5)	16
R5	Fast	11.2(3)	39.4(1)	47.1(4)	20
R6	Fast	10.9(4)	29.5(7)	49.6(2)	67
R9	Slow	9.0(5)	29.8(6)	38.7(6)	30
R8	Fast	8.8(6)	27.8(8)	48.0(3)	73
R7	Slow	8.7(7)	34.4(4)	33.4(7)	-3
R2	Slow	8.7(7)	26.1(9)	32.4(8)	24
R1	Slow	8.3(8)	30.6(5)	27.1(9)	-11

Note: The effects of 'family' were evaluated statistically by ANOVA and the Duncan's Multiple Range test. Solid vertical bars connect family means which are not significantly different at $P \leq 0.05$. For $GA_{4/7}$-treated families vertical bars are not used, here R4 and R6 differed significantly from R1 at $P \leq 0.05$. Family R8 was 'bushy' (had a high proportion of d.w. in lateral branches) except for $GA_{4/7}$-treated plants, where volume (and also dry matter) was reallocated to the main stem. See also table 2 in Ross and others (1983) for an example of a similar reallocation in *Pseudotsuga menziesii*.

[a] Based on unpublished research results of R. Pharis, R. Griffin, K. Eldridge, M. Slee, G. Nikles, P. Cotterill.

[b] Seed was obtained from controlled pollination crosses made at least 10 years earlier, and was stored until germinated in November 1981. Parents are of New Zealand origin and were all classed as superior phenotypes ("plus trees").

[c] Field growth ratings of "fast grower" or "slow grower" were given to each family on the basis of volume and height growth at age 9+ over a wide range of progeny tests in southeastern Australia.

[d] Plants were raised in a phytotron at 25°C day/20°C night under natural daylength (November 1981 to May 1982); all plants received supplemental incandescent light for 16 hr/day in the phytotron.

[e] Stem volume was calculated from height and circumference (1 cm above cotyledons), averages based on measurements of 10 plants for each family (age 138 days).

[f] Stem volume was calculated from height and diameter (12 cm above cotyledons). Averages based on measurements of about three plants for each of control and $GA_{4/7}$ treatment groups, for each family.

[g] Gibberellin $A_{4/7}$ (about 55:45 GA_4:GA_7), obtained gratis from Imperial Chemical Industries, was applied as a root drench at 200 mg per L pH 8.0 (60 ml per pot, every 6 days from age 132 days) to three seedlings of each family. As part of the paired test, equivalent numbers of seedlings received H_2O as a "control" treatment.

[h] Values in parentheses represent family ranking within each test or age class.

year, several hundred thousand to several million 'superior' seeds. Each of those seeds from superior families could in turn yield 10 to perhaps several hundred vegetative propagules for out-planting. And, if the vegetative propagation is accomplished during the first year after germination, then loss of juvenile growth potential due to 'maturation effects' will be minimal or negligible. The following discussion, and table 5, discuss briefly the possibility of early progeny testing of families produced from F1 controlled crosses. Although we do not discuss it herein, a number of techniques exist to propagate young seedlings, including traditional and tissue culture techniques. Indeed, it now appears that somatic embryos of Picea abies, and perhaps Pseudotsuga menziesii, have been produced from juvenile tissue, and if somaclonal variability is not excessive, somatic embryogenesis may offer an alternative and highly effective means of clonal multiplication of superior families and/or genotypes. (Durzan, D.J. personal communication).

The possiblity that inherent vigour in vegetative growth may be 'testable' at a very early age is shown by data presented in table 5 for Pinus radiata. Early stem volume growth differed significantly between families by day 138 from germination (table 5), and if Δ stem volume growth [Ross and others (1983, table 4)] or stem d.w. is used, the significance of the differences is even more pronounced (data not shown). Similar tests on Pinus caribaea (Pharis and others, unpublished) and Picea mariana (Williams 1985; Williams and others 1985, unpublished) lead to the same conclusion -- there are strong and significant correlations between early growth in a Phytotron or glasshouse environment and growth in the field at about age 10 years.

Between age 138 and 175 days the P. radiata seedlings appeared to be getting 'pot-bound', and the attractive correlation between rank order in the phytotron and growth rating in the field is less strong (for example, compare control values at age 175 days with values at age 138 days -- Families R6 and R8 have dropped to rank order 7 and 8 respectively, and Families R7 and R1, both slow growers in the field, have risen in rank order to and 5). However, for those plants which were treated with $GA_{4/7}$, Phytotron rank order still correlates very well with field growth rating (for example, the five fastest growing families in the phytotron are also fast growers in the field.

Hence, it appears that being 'pot-bound' may reduce stem volume growth (and other parameters also, data not shown) of some fast-growing families to a greater degree than slow-growing families. This lesion, however, appears to be 'cured' by application of $GA_{4/7}$ (table 5).

The $GA_{4/7}$ treatment causes an increased allocation of photo-assimilate to the main stem, often at the expense of the lateral branches for P. radiata (Pharis and others, unpublished) and Pseudotsuga menziesii (see table 2 in Ross and others 1983). Hence, families R6 and R8 may, under pot-bound or even normal conditions, have at least a modest deficit of endogenous GAs, or other mobilizing/growth factors. The 'other mobilizing/growth factors' may in turn be produced by or from endogenous GAs/exogenous GA application. The effect of $GA_{4/7}$ and/or high endogenous GAs could be as straightforward as providing more internodal volume in which to store photosynthate. Or GAs may have other or additional effects such as increasing ion uptake or 'mobilizing' photosynthate.

Thus, $GA_{4/7}$ application may be a useful additional tool to assist in discrimination between fast- and slow-growing families of P. radiata, and indeed $GA_{4/7}$ was also shown to be useful for this purpose with Picea mariana (Williams and others [1985], unpublished).

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POTENTIAL FOR CONTAINER SEED ORCHARDS

Stephen D. Ross, Andrea M. Eastham and Ralph C. Bower

ABSTRACT: Results are presented for Engelmann spruce and western hemlock which demonstrate the practical advantages of producing genetically improved seeds on small potted trees within a plastic-covered house. Relative to conventional soil-based orchards, these advantages include: earlier and more consistently abundant flowering; improved protection of cones and seeds; and strict control of pollen parentage, together with flexibility of clonal composition for maximum genetic gains. Because of more efficient space utilization and the greater ease and flexibility of management, production costs also promise to be lower.

INTRODUCTION

Potted trees, subject to strict control over environmental and treatment factors, have long been preferred by physiologists interested in studying the mechanism and control of flowering in conifers (e.g. Longman 1982; Ross 1985). Tree breeders, too, have occasionally capitalized on the relative ease with which precocious flowering can be induced, and controlled crosses subsequently made, using potted trees (Greenwood and others 1979). Until recently, however, there has been little serious interest in the management of small potted trees for volume production of genetically improved seed.

Since 1980, the British Columbia Ministry of Forests has been researching the development and evaluation of the indoor-potted seed orchards for western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and the interior spruces, Engelmann (*Picea engelmannii* Perry) and white (*Picea glauca* (Moench) Voss). With these species we faced (or would soon face) the same problems encountered with most conifers in attempting to produce genetically improved seeds in conventional soil-based orchards (Sweet and Krugman 1978; Ross and Pharis 1982). These included insufficient initiation of reproductive structures following a generally long "juvenile" phase; problems of pollination, including control of pollen parentage, and subsequent cone and seed development; and a host of management problems associated with tree size.

In this paper we review the potential advantages of indoor-potted seed orchards for more rapidly, completely and economically realizing the benefits of tree improvement. For convenience of discussion these are grouped into the three categories of production, genetic and management efficiency.

PRODUCTION EFFICIENCY

Initiation of Reproductive Structures

Many studies (Ross 1978, 1985; Tompsett and Fletcher 1979; Greenwood 1981; Bonnet-Masimbert and others 1982; Longman 1982; Philipson 1983) have demonstrated the relative ease with which potted trees can be induced to flower, given an appropriate stimulation treatment (see also Pharis and Ross in this volume). We illustrate this with two examples comparing, for western hemlock (table 1) and Engelmann spruce (table 2), the flowering response to induction treatments for potted and field-grown trees. Trees were vegetative propagules of mature plus-trees, with different clones and ramets of similar (spruce) or different (hemlock) ages, represented in the two orchard types. All treatment trees received spray applications of the growth regulator gibberellin $A_{4/7}$ ($GA_{4/7}$), calcium nitrate fertilizer and moderate drought (by withholding irrigation) appropriately timed for each species (Ross 1985 unpublished results). Potted trees of each species received these treatments both outdoors and in an unheated plastic-covered house (hemlock) or in a 30°C day:20°C night heated house (spruce). Heat treatment was also attempted for spruce in the soil-based orchard by enclosing grafts in a polyethylene tent.

Without treatment, flowering by both species in both orchards was rather poor. Treatment of western hemlock in the soil-based orchard increased from less than 5 to nearly 320 the mean number of seed-cone buds initiated per ramet, and from 27% to 100% the proportion of clones that flowered (table 1). However, the

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Table 1.--Comparison of 1985 flowering responses for 7-year-old potted and 12-year-old field-grown western hemlock rooted cuttings at the MacMillan Bloedel Harmac Tree Improvement Centre, B.C.[1,2]

Flowering response	Potted seed orchard[1]			soil-based seed orchard	
	Untreated	Treated			
	Outdoors	Outdoors	Indoors	untrt.	treated
Female flowering					
Ramets (=clones) Flowering (%)	75	100	100	27	100
Females/tree (no. $\pm$ s.e.)	52 ± 22	257 ± 65	427 ± 63	3 ± 2	319 ± 131
Male flowering					
Ramets (=clones) FLowering (%)	56	73	86	36	61
Mean Pollen Score[3]	1	1.6	2.2	1	1

[1] All treated trees received calcium nitrate fertilizer in spring and 6 weekly foliar sprays of 200 mg L^{-1} $GA_{4/7}$ commencing at vegetative bud burst. Potted trees, additionally, were subjected to a simultaneous 6 weeks of moderate drought

[2] One ramet per clone per treatment, with a different group of 22-23 parent-tree clones represented each orchard

[3] Pollen cone production scored: 0 = none, 1 = light, 2 = moderate, 3 = heavy

Table 2.--Comparison of 1985 flowering responses to gibberellin $A_{4/7}$, drought and heat treatments for 7-year-old potted and 8-year-old field-grown Engelmann spruce grafted ramets representing different parent-tree clones (Ross, Birzins and Cox, unpublished results)

Flowering response	Potted orchard (Victoria,B.C.)			Soil-based orchard (Vernon, B.C.)		
	Outdoor	$GA_{4/7}$ + drought		Untrted	$GA_{4/7}$ + drought	
	Control	Outdoors	Indoors	Control	Alone	Tented
Ramets (clones)/trmt (no.)	16(16)	16(16)	16(16)	1489(296)	193(193)	410(209)
Female flowering						
Ramets producing (%)	12	69	75	10	17	24
Clones producing (%)	12	69	75	23	17	24
Cones/tree (no. $\pm$ s.e.)	1	30 ± 9	54 ± 33	1 ± 1	2 ± 1	11 ± 4
Male flowering						
Ramets producing (%)	19	81	88	4	16	15
Clones producing (%)	19	81	88	19	16	23
Cones/tree (no. $\pm$ s.e.)	1	44 ± 10	33 ± 9	2 ± 2	2 ± 2	2 ± 2

much younger (7 vs. 12 years) potted trees initiated in response to treatment indoors 33% more seed-cone buds each than the treated field-grown trees. Outdoors, the potted trees were less responsive to treatment, although here also 100% of the clones flowered.

The difference in treatment response was even more dramatic for Engelmann spruce where the grafts in the two orchards were of similar ages (table 2). As found by Chalupka and Giertych (1977) for Picea abies (L.) Karst., heat treatment by means of tenting significantly enhanced female flowering in the soil-based orchard, although still only 24% each of the ramets and clones produced seed-cone buds. In contrast, nearly 90% of the clones whose potted ramets received heat plus $GA_{4/7}$ treatment indoors flowered, and their mean production of seed-cone buds was almost four times that of the comparably treated field-grown trees.

As is typical for young soil-based orchards, pollen production here by both species was very sparse in relation to female flowering. In contrast, the smaller potted trees produced pollen in abundance. Furthermore, a significantly greater proportion of the clones contributed to this more profuse male flowering by potted trees, this again being particularly dramatic for interior spruce (table 2).

Where potted trees are properly managed (see below), there is no reason to assume that profuse flowering cannot be consistently achieved on a biennial basis. The potted trees in both studies reported here had flowered nearly as profusely in response to essentially the same treatments applied two years previously. This, however, was a first-time attempt at stimulation of the field-grown trees. Retreatment of a soil-based orchard may or may not be successful, depending on climatic conditions in the year of stimulation (Wheeler and others 1985). Adverse site and climatic factors can negate even the most effective of treatments, including applications of $GA_{4/7}$ in conjunction with nitrogen fertilizer, girdling and root-pruning (see Pharis and Ross in this volume).

High temperature and water stress generally appear to be the most important requirements for abundant flowering in many conifers (e.g. Pollard and Portlock 1981; Ross 1985). Their timing is also critical, as the results for Engelmann spruce in figure 1 clearly show. Cone-bud differentiation in this species is known to occur during the late stage of slow shoot elongation, and it is only at this time that heat treatment promotes flowering. Applied earlier, while shoots are rapidly elongating, its effect on flowering is strongly inhibitory, although water stress is highly promotive at that time and only then. This optimal sequence of early drought and late high temperatures seldom occurs in nature but is easily created in an indoor-potted orchard.

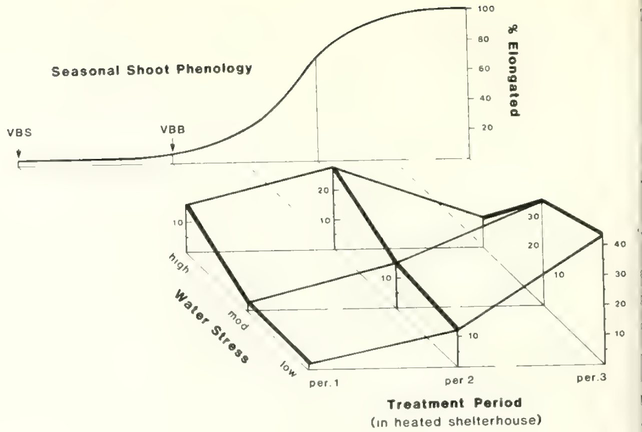

Figure 1.--Effect of heat and drought treatment timing on female flowering in young potted Engelmann spruce grafts. Ramets were moved into a 30° C day:20° C night heated shelterhouse at different stages of lateral shoot elongation (VBS and VBB refer to vegetative bud swelling and burst, respectively), during which they were either kept well watered or subjected to a moderate or severe drought by withholding irrigation until their midnight needle water potential had decreased to -0.75 or -1.5 MPa (adapted from Ross 1985).

Cone and Seed Efficiency

The ability to protect developing cones and seeds from adverse climatic conditions (high as well as low temperatures and wind) is another important advantage of indoor-potted orchards (see Bramlett in this volume). The ready accessibility of cones on small potted trees for inspection and spraying should also result in more effective insect and disease control.

Table 3 compares cone and seed traits for potted ramets of the same western hemlock clones that were induced to flower and subsequently maintained either outdoors or in a plastic-covered house without supplemental heat. Not only did the trees outdoors initiate significantly fewer seed cones, but the proportion of those that survived was also significantly lower than indoors. This was the result of several severe freezes during winter and early spring. Outdoors, the surviving cones contained fewer total (filled plus empty) seeds as well, probably for the same reason. Possibly the different conditions of heat and water stress under which trees were induced to flower indoors and outdoors the previous year had a carry-over effect on subsequent cone and seed development. However, our results suggest that so long as trees are not overly stressed during induction such carry-over effects are relatively small.

In a soil-based orchard, especially a young one, pollen is likely to be limiting for good seed set (see tables 1 and 2). This was not a

able 3.--Cone and seed traits compared for potted western hemlock rooted cuttings induced and maintained outdoors or in an unheated greenhouse (Eastham and Ross, unpublished data)[1,2]

Trait	Outdoor ($\bar{X}$±s.e.)	Indoor ($\bar{X}$±s.e.)
ones initiated/tree (no.)	320±23	633±30
urviving cones/tree (no.)	198±13	529±26
one efficiency (%)	62	84
otal seed/cone (no.)	27±1	31±1
illed seed/cone (no.)	10±1	14±1
eed efficiency (%)	37	45
00-filled seed wt. (mg)	200±5	199±5
8-day germination (%)	79±5	82 ±5

Rooted cuttings were 7-years old at time of induction, with 3-8 ramets each of the same 8 plus tree clones

See footnote 1 of table 1 for description of induction treatment.

onsideration in the present comparison of ndoor and outdoor potted trees (table 3). nbagged female strobili on both groups of rees were supplementally pollinated at least hree times when maximally receptive with the ame pollen lot (from potted ramets indoors). ven then, however, the filled seed percentage as significantly lower outdoors. Cool, moist onditions prevailed outdoors throughout the ollination period and this could have dversely affected pollen germination and ubsequent fertilization of ovules.

otted trees in this study were maintained in he plastic-covered house following ollination. However, this does not appear to e necessary, or in the case of some species, articularly desirable for good subsequent cone nd seed development. Where flowering ngelmann spruce grafts were subject to levated temperatures within an unheated house, he resulting cones were significantly smaller elative to ramets whose cones matured outdoors Ross, in prep.). These cones also contained ignificantly fewer total seed, of which a maller percentage was filled.

or this species, and presumably most conifers, ptimal conditions for cone and seed evelopment are the same as those that favor igorous vegetative growth-- that is, abundant ater and nutrients along with moderate emperatures. These are not the conditions hat promote flowering. Another advantage of orking with potted trees, therefore, is that hey may be managed separately for each nitiation and subsequent development of eproduction structures to ensure maximum roduction of high quality seed. This is not enerally possible in a soil-based orchard.

GENETIC EFFICIENCY

Control of Pollen Parentage

It is no secret that the wind-pollinated orchard is not very efficient when it comes to capturing the genetic benefits from tree improvement (Sweet and Krugman 1978; Smith and Adams 1983; El-Kassaby and others 1984). Dilution of genetic gains from contaminating foreign pollen is a serious problem in many such orchards. Where orchards are located off site, the seed produced may also be maladapted to the planting region. Furthermore, only a relatively small proportion of the orchard parents may be contributing male and female gametes. Of these an even smaller proportion may have the opportunity to mate due to the nonsynchrony in timing of pollen shedding and female receptivity among clones. The situation is thus ripe for selfing and other departures from truly panmictic mating, with potentially deleterious effects on realized genetic gains.

Indoor-potted orchards, on the other hand, allow a degree of control over pollen parentage not feasible in conventional wind-pollinated orchards to achieve maximum-possible genetic gains. The approach to pollen management will depend to a large extent on the status of the breeding and testing program.

Artificial pollination may not be warranted when dealing with untested clones. But even then positive steps can be taken to ensure more nearly panmictic mating. At the very least, the potted trees can be effectively isolated indoors from foreign pollen. And, it may be expected that a larger proportion of clones will be contributing male and female gametes than in the soil-based orchard (tables 1 and 2), which should reduce the potential for self pollination. Reproductive bud development in spring can be synchronized, either hastened or slowed as required for late- and early flushing clones, respectively, by moving their potted ramets into a warmer or cooler house.

It is, however, where information on the mating value of individual orchard clones is available that the genetic benefits from pollen management in indoor-potted orchards will be greatest. This may involve supplemental mass pollination using pollen collected from the very best parents. Even more attractive is the opportunity to mass produce progeny of elite full-sib families through controlled crossing, and thus capitalize on that portion of the nonadditive genetic variance associated with specific-combining effects.

Unlike the problems encountered with large trees in soil-based orchards (see Sweet and Krugman 1978), artificial pollination is relatively easy with small potted trees. Certain clones (and even ramets within clones) have a tendency to initiate mainly seed cones or pollen cones, and these may be managed separately as female and male parents. In

early spring the female parents might be moved outdoors to slow their reproductive bud development relative to pollen parents left in an unheated house. This will ensure the necessary lead time for collection and processing of pollen from all clones prior to the onset of female receptivity (J.E. Webber, pers. com.). The pollen is easily harvested, either by picking individual pollen cones as they mature, or shaking the tree and collecting the shed pollen on a sheet of paper. We have found the latter method to be particularly convenient for species, such as western hemlock, which have very small pollen cones. The female parents are then moved back indoors for artificial pollination at the optimal time with high viability, fresh pollen.

Infusion of New Selections into Production

By the time a conventional orchard comes into full production, 10 to 15 or more years after establishment, its seed may already be genetically obsolete. Even if progeny test results are not available before then, most orchards will have already required a silvicultural thinning by that age. The opportunity to use these results to rogue inferior clones from the orchard therefore may be limited as well. With an indoor-potted orchard the lag time between selection and seed production for new clones is considerably shorter. Also, unlike conventional orchards, whose clonal composition is determined at time of establishment, the potted orchard may be continually upgraded genetically as new selections become available. It is not only more efficient genetically, but far less expensive as well to replace individual potted ramets than an entire soil-based orchard.

We call this in situ advancing-front, and the concept of orchard generations no longer applies (Ross and Pharis 1982). In the case of a new tree improvement program, the potted orchard would probably contain ramets of all plus-trees in sufficient number to meet projected seed requirements over, say, the next 10 years. Breeding and seed production could occur simultaneously, but with primary emphasis given initially to the former so as to minimize delays in progeny test establishment. Progressively more severe roguing of inferior clones would then occur over time as the progeny tests become older and their results more reliable. Initial roguing of parents could perhaps begin on the basis of four year or younger progeny test results, with selection among progeny of the best families occurring several years later (Lambeth 1980; Pharis and Ross in this volume). The clones thus eliminated might be replaced initially by extra ramets of the proven parent clones (as required for seed production), but ultimately by ramets of new advanced-generation selections. Even then, the potted orchard could still contain some highly superior parents from previous generation(s).

MANAGEMENT EFFICIENCY

Production Costs

Indoor-potted orchards may be more efficient than soil-based orchards in terms of providing earlier production of seed of higher genetic quality, but we are frequently asked are they practical and cost effective? We are only just beginning to acquire comparative cost-benefit data for the two types of orchards, but for western hemlock and interior spruce the answer does appear to be yes.

Consider the hypothetical case of two interior spruce orchards, one potted and the other soil based, each with a production capacity of five million viable seeds per year. Using Birzin's (this volume) expected yield of 4,000 viable seeds per ramet per annum by age 15 years after grafting, and a final spacing of 5m x 5m (1250 ramets rogued from an initial 2500), the soil-based orchard would occupy nearly 3.5 ha, exclusive of roads and support facilities. Our results indicate that each interior spruce ramet in an indoor-potted orchard is capable of producing on average 3,000 viable seeds every other year beginning at age 7 years in response to biennial induction treatment. Thus, a potted orchard with the same five-million annual production capacity would contain about 3,300 ramets but only occupy 700m^2 of covered houses and a like area of outdoor container yards. (Only half the ramets would be indoors at any one time-- for cone induction and pollination-- except possibly for freeze protection over winter when they can be tightly packed to conserve space.)

Even a very superficial analysis indicates that the potted orchard will probably be less costly to establish. One does not require a sophisticated controlled-environment greenhouse -- a plastic-covered house with propane heater and let-down sidewalls for natural ventilation will suffice. In this example, the cost to construct two such houses (10m x 35m) and a 700 m^2 outdoor container yard, each equipped with movable pallets and automated drip-irrigation system, should not exceed $45,000 (costs in 1985 Canadian dollars). Assume another $8,000 to propagate the additional 800 ramets which the potted orchard requires (3300 vs. 2500 initially for the soil-based orchard).

However, the potted orchard requires little space. It can be sited anywhere, on relatively inexpensive and otherwise nonproductive land-- perhaps in conjunction with a container nursery where certain facilities and equipment can be shared. On the other hand, proper site selection is crucial to the success of the soil-based orchard (Birzins, this volume). And, sites conducive to abundant flowering tend to be in short supply and high demand for agricultural use. Such land in the Okanagan Valley of interior B.C. currently goes for about $17,000 per hectare (Birzins, pers. comm.), for a total purchase price of nearly

0,000 for the 3.5 ha orchard in this ample. That does not include site eparation, road construction, fencing or rigation systems.

e indoor-potted orchard is equally attractive om the standpoint of potentially lower erating costs. Contrary to popular belief, ntainer culture for seed production need not highly labor intensive. Much of the work otting and plant handling, irrigation and plications of fertilizers, pesticides and s) can be automated to a large degree. There e the additional expenses for pots, media and ating, but these promise to be small in lation to the large amounts of fertilizers d other chemicals and water used in il-based orchards. Finally, there are large onomies to be realized in the induction, llination, protection and harvesting of cones en working with small, potted trees.

comparing the two orchards one must also nsider the difference in time and value of ed produced. There are two costs associated th the longer nonproductive phase of the il-based orchard (15 vs. 7 years for the tted orchard in this example). There is the ne-discount factor and the opportunity cost delayed realization of genetic benefits. this example, the indoor-potted orchard uld already have produced 40 million viable ed by the time the soil-based orchard came to commercial production. That relates to proximately 16,000 extra hectares of new terior spruce plantations containing the very st possible genetically improved trees.

oduction Flexibility

loor-potted orchards offer a unique exibility of management. Their production pacity can be rapidly scaled upwards or wnwards in response to changing seed quirements. The mobility of potted trees so allows for most efficient site lization. Unlike soil-based orchards with eir fixed-tree arrangement, the potted chard can start off small, and then be panded as needed to accommodate the creasing size of trees.

other advantage of indoor-potted orchards ates to a point made by Libby (1985). He tes that "Seed-orchards are sensitive to onomies of scale, and one can rarely justify seed-orchard for local low volume demand." en with so-called 'major' species having a ge total annual seed requirement, this oduction is often divided among many breeding nes each represented by its own small chard. Several of these may be consolidated a single site for increased management iciency, but then there is the possibility t seed will be maladapted to their site of lization due to cross-pollen contamination ween the different breeding zones. Trees m many breeding zones may be managed as a single group in a potted orchard, except when separated for pollen management.

In a potted orchard one can also conceive of utilizing controlled pollinations to capitalize on those unique characteristics of individual clones (such as disease or drought resistance or special wood properties), of the same or different breeding programs, to custom produce progeny that are specifically adapted to certain problem sites or for minor, but valuable end products.

Finally, potted orchards are also most attractive for those minor species whose annual seed requirements hardly justify a seed-orchard program, but which are poor seed producers in nature. _Chamaecyparis nootkensis_ (D. Don) Spach, a species not widely planted but still highly prized for its quality wood, is an excellent example. In containers this species flowers profusely at a very young age in response to GA_3 treatment (Bower, unpub. data). A desirable strategy for such a species might be to rapidly build up a number of years' supply of seed in a small orchard, and then discard the potted ramets which could easily be repropagated when the seed supply again runs low.

CONCLUSIONS

Compared to conventional orchards, indoor-potted orchards offer the potential for attaining earlier, more reliable seed production and maximum-possible genetic gains through sexual reproduction, all with a much greater efficiency of management. The biological feasibility of producing genetically improved seed on small, potted trees is now well established for many conifers. And, further research will lead to improved efficiencies of production and management. However, for western hemlock and the interior spruces this research has progressed to the point where we are now ready to begin pilot testing the approach for cost effectiveness on a semi-operational scale.

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MANAGING BLACK SPRUCE SEEDLING SEED ORCHARDS FOR CONE AND SEED PRODUCTION

Ronald F. Smith

STRACT: The use of fertilizers to stimulate ne production in black spruce (Picea mariana ill.) B.S.P.) seedling seed orchards is dis- ssed. The types, rates, and time of fertilizer plication are reviewed, with emphasis on the uses of inconsistencies in responses to ferti- zer treatments. The interactions between ini- al tree spacing and the time and degree of gueing and tree response to fertilizing are iefly reviewed.

TRODUCTION

ı New Brunswick, seedling seed orchards are tablished on 'typical' planting sites. Although edling orchards are not managed as intensively clonal orchards, cultural practices such as rtilizing to enhance cone production will be cessary for these orchards to be fully oductive.

plying fertilizer is the most common technique rrently employed for enhancing cone production seed orchards. However, no one type of ferti- zer or rate of application has been successful all instances (Sweet and Hong 1978). The fectiveness of any fertilizer treatment in hancing cone production varies with tree size, ee spacing, the type of fertilizer used, the te, method, and timing of application, the ather immediately following fertilizer applica- on, and the genetic predisposition of the trees produce cones.

rtilizer and spacing experiments were estab- shed in 8-to 10-year old black spruce (Picea riana (Mill.) B.S.P.) plantations from 1980- 82 (Smith 1983). This paper summarizes some of e factors that influenced the effectiveness of plying fertilizers to enhance cone production d discusses the results as they apply to manag- g seedling seed orchards.

per presented at the Conifer Tree Seed in e Inland Mountain West Symposium, Missoula, , August 5-6, 1985. Paper presented by . G. Edwards, Canadian Forestry Service, cific Forest Research Centre, Victoria, .

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FACTORS AFFECTING RESPONSE TO FERTILIZING

Tree Size

Female and male cone production were positively correlated with both tree height and diameter, but the correlations were higher for diameter (Smith 1983). Small trees did not respond as well to fertilizer treatments as did large trees (fig. 1). In some instances, small trees did not respond at all to treatment regardless of the type or rate of fertilizer applied.

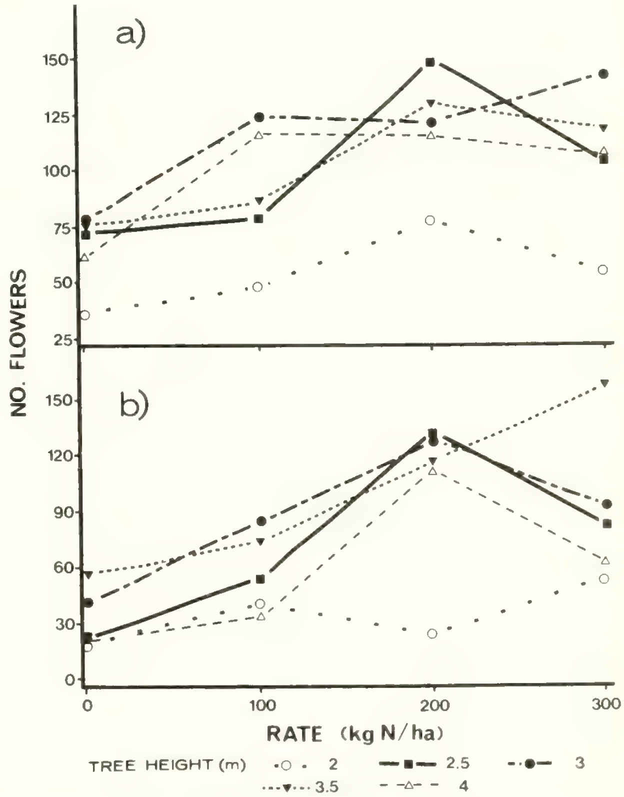

Figure 1. -- Relation between a) female and b) male cone production in black spruce (1982) and tree height and the amount of ammonium nitrate fertilizer applied in 1981 (May - June).

Tree Spacing

Tree spacing affects the capacity of seed orchard trees to respond to fertilizer treatments in that trees growing at wider spacings have fuller crowns with more potential flowering sites (greater numbers of buds). Fertilizing did not increase the number of buds, but rather the proportion of buds which developed reproductively (Smith 1985).

The degree to which spacing will limit response to fertilizing differs between species. In red pine, (Pinus resinosa Ait.) female cones can be borne on a large portion of the live crown. The number of cones per tree may increase with increased spacing until the total number of cones per unit area decreases due to the reduced number of trees (Stiell 1971). In young black spruce however, female cones were generally borne in only the top three or four whorls. The number of potential flowering sites in the upper crown limited the degree to which female cone production increased in response to wider spacings. However, trees at wider spacings did produce more cones of both sexes (fig. 2).

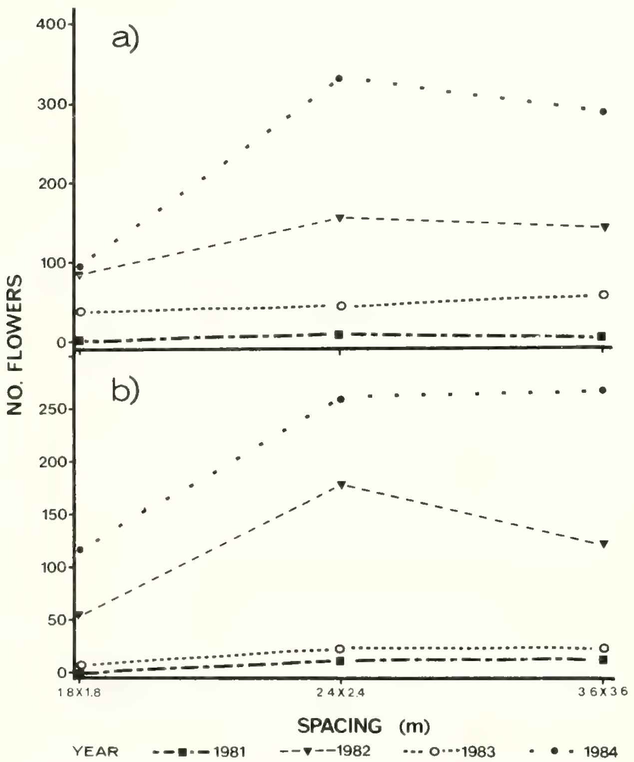

Figure 2. -- Effects of spacing on a) female and b) male cone production in black spruce.

Seedling seed orchards are often planted at close spacing, e.g., in New Brunswick, 1 X 2 m (3 X 6 ft) or 1.5 X 2 m (4.5 X 6 ft). Rogueing removes genetically 'inferior' families (trees) thus allowing the remaining trees to develop full, vigorous crowns capable of supporting large cone crops. However, growth rate of the trees affects the time and intensity of the rogueing, as trees must be removed before growth and, concomitant , seed production within the orchard is affected Orchards located on very fertile sites may require rogueing earlier and to a heavier degree than might be justified from the family test measurements alone.

Type of Fertilizer

Nitrogenous fertilizers, particularly those co -aining the nitrate (NO_3) form of nitrogen, e.g ammonium nitrate and potassium nitrate, have b n most successful in stimulating cone crops (Puritch 1977). Applying ammonium nitrate increased both male and female cone production i black spruce whereas applying urea did not (Sm h 1983).

Rate of Application

The rate at which fertilizer is applied determines whether or not flowering will be affecte and if so, positively or negatively. Fertilizi black spruce at rates greater than 300 kg N/ha decreased both female and male cone production but especially the latter (fig. 3). Both the amount of fertilizer required per tree to elic the maximum cone production response, and the rate at which overfertilization occurs, increas with tree size (Ebell 1972a).

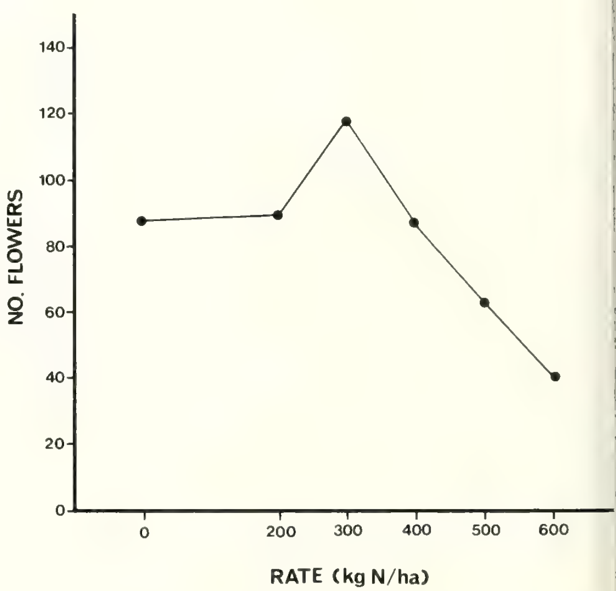

Figure 3. -- Relation between rate of ammonium nitrate fertilizer application and male cone production in 1982 for black spruce trees ferti lized in 1980 (from Smith 1983).

Method of Application

The amount of fertilizer applied is usually expressed as the total amount of fertilizer or nutrient per unit area. However, the effectiveness of fertilization in stimulating cone produc

tion is determined by how much of the applied fertilizer each tree receives. Fertilizer should be placed under the crown dripline because the bulk of a tree's root system lies within this area. Band-type spreaders are better than cyclone types because there is better control of fertilizer placement.

Broadcast applications are more effective for large than for small trees as their root systems occupy more of the site. If a broadcast method is used, more fertilizer per hectare may be needed to elicit a flowering response, i.e., the amount of fertilizer lost to uptake by other vegetation will be more than if the same total amount of fertilizer was applied, but placed in a band around each tree. When accessibility within the orchard precludes using broadcast methods, hand applications are necessary. Hand applications allow for rates to be increased for large, and decreased for small trees, respectively, which should optimize the flowering response.

Timing

The time that trees are fertilized will determine whether vegetative growth, reproductive growth, or both, will be affected. Fertilizer must be applied before the reproductive buds for the next year are formed (primordia differentiation). In Douglas-fir, April and May fertilizer applications significantly increased cone production whereas June applications did not (Ebell 1972b), because primordia differentiation in Douglas-fir occurs in late May to June (Owens 1969). Owens and Molder (1979) give growth and development patterns for the major North American genera. These general guidelines could be used by orchard managers to determine approximately when differentiation occurs, enabling them to establish approximate 'not-later-than' dates for fertilizer applications when the exact phenology for their species and orchard sites is not known.

In black spruce, applying fertilizers up to two months prior to the approximate time of primordia differentiation still significantly increased cone production the following year (Smith 1983). In southern pine orchards, fertilizer can be applied as much as one month earlier than the 'recommended' times for female cone induction (Schmidtling 1983) conferring the advantage of coordinating fertilizer applications to periods of reduced workloads.

Effects of Weather

Response to fertilizing is usually best when the weather conditions during the year of application are conducive to the initiation of strobili, e.g., the response year is a 'good' cone crop year. In black spruce, trees did not respond to fertilizing as well in naturally 'poor' flowering years as in 'good' years; only the larger trees showed an increase in cone production in these 'poor' years.

Weather influences the rate of fertilizer uptake and the total amount of nutrient which actually becomes available to the tree roots. Heavy rainfall immediately after applying fertilizer can cause a high proportion of the fertilizer to be leached through the soil. When this occurs, the cone-induction effect of the applied fertilizer can be lost. The cone-induction effect of fertilizing can also be lost under warm, dry conditions, i.e., fertilizer will deliquesce more slowly, perhaps remaining in the soil longer. When this occurs it also takes longer for the fertilizer to reach the root surfaces. If fertilizer is applied close to the time of primordia differentiation, the proportion of the fertilizer which actually reaches the roots in time to affect cone production could be reduced, thus reducing its effectiveness in stimulating flowering. When this occurs, the rate at which fertilizer should be applied to maximize cone production must be increased (Ebell 1972b).

Genetic Effects

Probably the most important factor influencing cone production in seed orchards is the genetic predisposition of the trees to flower. Differences between clones account for a large proportion of the total variation in flowering in seed orchards (Sprague and others 1979; Schmidtling 1983). Consequently, genetic effects can mask the effects of fertilizer treatments. Adding nitrogen can increase the numbers of flowers produced, but will generally not induce those trees to flower which were not 'predisposed' to do so (Robinson 1979; Barnes and Bengston 1968).

Genotype-fertilizer interactions at the family level have been reported for conifers (Jahromi and others 1976; Maliondo and Krause 1985). The effectiveness of fertilizer treatments in inducing cone production for different families is not well documented. The strong fertilizer-clone interactions in reponse to applying nitrogen fertilizers (Robinson 1979; Sweet and Krugman 1977) would indicate that family differences can be expected. It is, however, impractical on an operational scale to formulate fertilizer recommendations on a family basis. Consequently the fertilizer and rate which is effective for 'most' families should be used.

The only means of managing the genetic component within seedling seed orchards is through selecting which families or individuals are to be removed. Fecund individuals within the best families can be favored over nonbearing trees given that these trees also exhibit good growth characteristics. Similarly, trees which respond well to cone-induction treatments may be favored over those which do not respond well. Flowering records, by family, should be kept to evaluate accurately fecund families and trees within the orchard.

CONCLUSIONS

The following practices should be followed if the maximum benefit from applying nitrogen fertilizers to stimulate cone production in black spruce seedling seed orchards is to be realized.
1. Orchard rogueing must be scheduled such that tree spacing never limits crown development and, concomitantly, the capacity of the trees to respond to cone-induction treatments.
2. The type of fertilizer used, and the rate, method, and timing of application must be considered in planning fertilizer schedules.
3. Records of flowering in the orchard should be kept so that the final rogueings favor not only the best families (based on family test measurements), but also the more fecund trees within these best familes.

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VARIATION IN CONE AND SEED PRODUCTION FROM NATURAL STANDS, PLANTATIONS, AND CLONAL-BANKS OF LODGEPOLE PINE

Cheng C. Ying and Keith Illingworth

\BSTRACT: Information reported in this paper is)ased on: 1) 780 parent trees from 53 provenances)f the inland form of lodgepole pine (Pinus contor- :a ssp. latifolia); 2) a wind-pollinated progeny)lantation of 778 families derived from (1),)lanted in 1973, and in which conelet production ,as recorded in 1979, 1980, and 1981 (age 10, l1, and 12 from seed); and 3) 160 clones (800 ;rafts) in two clone banks, which were planted .n 1972, and in which conelet production was :ecorded annually since establishment. Both (2) ınd (3) are located at Red Rock, south of 'rince George, British Columbia.

'he results suggest that:

1. a managed clonal seed orchard can roduce commercial quantities of seeds (over 200 ones per graft) in 10 years;
2. a clonal orchard may produce better uality seeds than natural stands (grafts roduced 44% more seeds per cone and seeds 48% eavier than did natural stands);
3. large clonal variation in both seed- and ollen-cone production capability will not only ffect the genetic composition of seed orchard eeds, but also the balance between maximizing enetic gain and maintaining seed production apacity at the time of seed orchard roguing;
4. differential cone production capability mong provenances is inherited rather than nvironmentally induced, and that provenances of orthern latitude origin are more precocious but ess prolific than the southern latitude ones;
5. the current strategy of concentrating eed orchards for the central Interior at Red ock and for the southern Interior at Vernon ppears to be appropriate biologically and conomically, in view of the strong geographic rend among provenances in cone production apability, particularly of pollen cones;
6. seed orchards for northern British olumbia and the Yukon probably should not be ocated south of latitude 56°N in view of their oor growth at many sites in the central and outhern Interior British Columbia.

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per presented at the Conifer Tree Seed in the .land Mountain West Symposium, Missoula, MT, gust 5-6, 1985.

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INTRODUCTION

This paper reports geographic and year to year variation in conelet production and seed yield of lodgepole pine in natural stands, in a wind-pollinated (w.p.) provenance-progeny test plantation, and in two clone banks, emphasizing their practical implications for seed orchard planning.

Lodgepole pine has become a major planting species in the Pacific Northwest. In the interior region of British Columbia alone, planting of lodgepole pine reached 15 million seedlings in 1983 (i.e., 20% of the total seedlings planted), and is projected to reach 73 million seedlings (40% of the Interior program) at the turn of the century. The goal of planting only genetically improved trees by the year 2000 (B.C. Ministry of Forests 1980) has led to the rapid expansion of a tree improvement and seed orchard program in the British Columbia Interior. Seed orchards are the most expensive phase of a tree improvement program and their efficiency determines, to a large extent, the cost-benefit ratio of such a program. Information reported in this paper provides a basis for improving the efficiency of lodgepole pine seed orchard planning in terms of their location, size, and projected seed yields.

SOURCE MATERIAL AND DATA COLLECTION

Cone production and seed yield data were gathered from three sources:

1. about 780 parent trees from 53 provenances of the inland form of lodgepole pine (Pinus contorta ssp. latifolia) (Critchfield 1980). The majority of the provenances comprised 15 parent trees. The number of seeds per cone and 1000-seed weight were determined for each parent tree;
2. a wind-pollinated progeny plantation of 778 families derived from (1). The plantation was established in 1973 with 2+1+1 stock, and was laid out according to a compact-family (split plot) design (provenance designated as main plot and family the sub-plot with three replications of 6-tree family plot). Spacing was 3.7 x 3.7 m. Seed- and pollen-cone production were recorded by counting the number of conelets and pollen clusters in the spring of 1979, 1980, and 1981 (age 10, 11, and 12 from seed) as follows:

Year	Prov.	Number of W.P. fmlies	Trees
1979	53	778	8888 (in 2 reps)
1980	53	778	8835 (in 2 reps)
1981	10	148	828 (in 1 rep)

Various numbers of pollen clusters were sampled from many flowering trees to determine the average number of microstrobili per pollen cluster for each family and provenance.

3. one hundred and sixty clones (800 grafts) in two clone banks, named SCA and SK. Grafting was done in 1971 and 1972, and both clone banks were established in the fall of 1972 with five ramets per clone in a single row, spaced 3.7 x 3.7 m. The two clone banks were planted side by side. SCA contains clones from the north, and SK from the south, of latitude 56°N approximately (fig. 1), and 335 of the 375 grafts in SCA (75 clones) and 337 of the 425 grafts (83 clones) were living in 1985. Seed- and pollen-cone production were recorded every year since planting, and in 1981 seed yield and seed weight were determined for a sample of 20 clones representing their geographic distribution (Ying and others 1985b).

Both the w.p. progeny plantation and the clone banks are located at Red Rock (lat. 53° 46'N, long. 122° 42'W, elev. 580 m), south of Prince George. The climate at both sites is similar, but the soils are very different: the clone banks are located on a deep, freely drained silty sand, the progeny plantation is on a stony glaciofluvial terrace.

Geographic locations (fig. 1) of parent trees in (1) and (2) and ortets of 3) are summarized below:

Source	Lat.(N)	Long.(W)	Elev.(m)
(1 & 2)	49°04'-63°18'	114°25'-136°18'	455-181
(3)	49°18'-63°22'	120°10'-136°17'	250-147

Data were subjected to variance analyses, and correlation and multiple regression were employed to elucidate the relationship of cone production at different ages and with the geographic origin of provenances.

SEED YIELD AND SEED WEIGHT

Both seed yield (i.e., number of seeds per cone) and seed weight showed large variation from

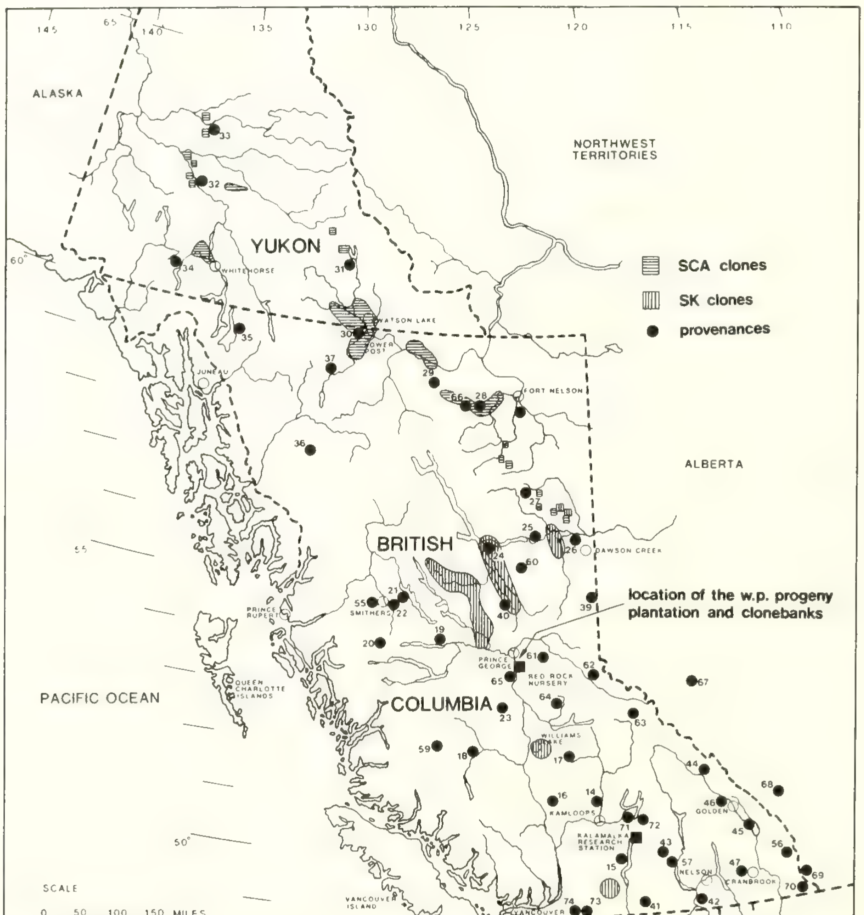

Figure 1.--Geographic origin of the 53 provenances and the ortets in SK and SCA clone banks.

Table 1.--Comparison in number of seeds per cone and 1000-seed weight between natural and grafted lodgepole pine

Geographic region	No. seeds per cone: Natural stands	No. seeds per cone: Grafts	1000-seed weight (mg): Natural stands	1000-seed weight (mg): Grafts
Yukon and Northern B.C.	22	24	2.6	4.1
Southeastern B.C. and Alberta foothills	12		3.2	
Central and Southern B.C.	16	22	2.8	3.8
Coast-interior transition	11		2.5	
Mean	16	23	2.8	4.0
Range (provenance means)	9-31		2.2-3.9	
Range (tree or clone means)	1-64	5-39	1.4-4.6	3.3-4.9

ovenance to provenance, tree to tree, or clone clone (table 1). Variance analyses indicated % among- versus 60% within-stand variation. afts produced 44% more seeds per cone and ese were 48% heavier than trees in natural ands (table 1).

gnificant and positive correlations between mber of seeds per cone and latitude and ngitude (table 2) suggest a northwest-utheast geographic trend: trees from the kon Territory and northern British Columbia oduced the highest number of seeds per cone, d those from Alberta, southeastern British lumbia, and near the coast-interior transition ne were among the lowest (table 1). An posite geographic trend was evident in seed ight (table 2): trees from Alberta produced e heaviest seed and those from the Yukon and ar the coast-interior transition, the lightest able 1). However, the range of variation in ed weight was rather small (table 1). This nfirms the conclusions of Birot (1978) and tchfield (1980) that variation in seed weight largely a character of the subspecies. titudinal and longitudinal trends were not as vious in the clone banks probably due to the all number of clones (20) studied and the rge within-provenance variation (Ying and ners 1985b). Results from both the clone nks and natural stands indicated poor seed eld of high-elevation trees.

le 2.-- Correlation of number of seeds per cone and 1000-seed weight of natural lodgepole pine trees with latitude, longitude and elevation of their origin (based on provenance means, n = 53)

	No. seed per cone	1000-seed weight
itude	.66 a	-.32 b
gitude	.50 a	-.60 a
vation	-.38 a	.18

ignificant at 0.01 level.
ignificant at 0.05 level;

SEED- AND POLLEN-CONE PRODUCTION

Grafts

Seed- and pollen-cone production were recorded in the clone banks over a 12-year period (fig. 2); both seed- and pollen-cone production increased steadily after planting except for the unexpected decline in 1983. Most grafts produced a commercial quantity of cones (over 200 conelets per graft) 10 years after planting. Pollen-cone production, although about 5 years behind initially, reached the level of commercial quantities at about the same age as seed-cone production, and therefore would not affect the commercial production of a clonal seed orchard (fig. 2).

Grafts in the SCA clone bank (northern latitude origin) started to produce both seed and pollen cones earlier, but were eventually out-produced by those in the SK clone bank (southern origins) (fig. 3).

Seedlings

Seed- and pollen-cone production of the 10 provenances (148 families) counted in all 3 years (1979-81) are presented in table 3. Pollen-cone production showed a sharp increase from 1979 (age 10) to 1980 (age 11), and the increase from 1980 to 1981, though not as spectacular, was still substantial, with the exception of #31 from the Yukon. Average number of pollen clusters per living tree in 1981 was 25 times that in 1979 (table 3). Compared with pollen-cone production, changes in seed-cone production from 1979 to 1981 were relatively small: most provenances showed a moderate increase from 1979 to 1980, but decreased from 1980 to 1981 (table 3). The range of provenance difference in pollen-cone production was much larger than that for seed cones. For example, in 1981 the most prolific provenance produced almost 10 times more pollen cones than did the least prolific one, excluding the atypical provenance #31, but the ratio of difference

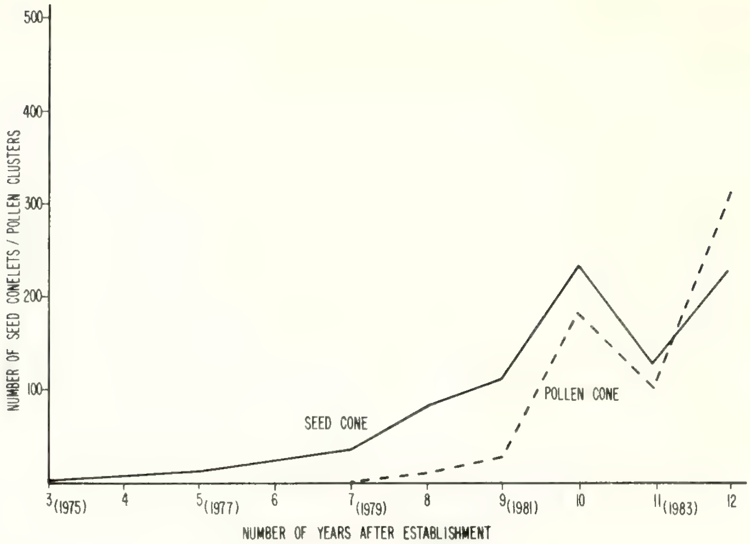

Figure 2.--Average yearly seed- and pollen-cone production in the two grafted clone banks.

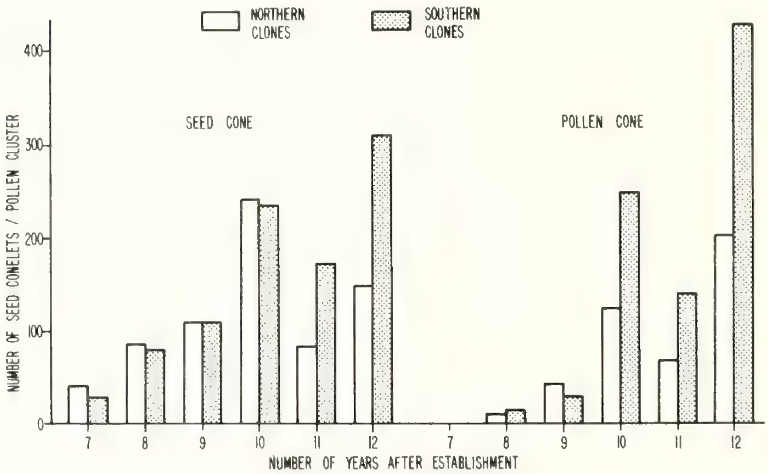

Figure 3.--Comparison in seed- and pollen-cone production between clones of northern latitude (SCA) and southern latitude (SK) origin.

between the most and the least productive provenances was only about 2 to 1 for seed-cone production (table 3). The change of the pollen cone - seed cone ratio from 0.9 at age 10 to 10.5 at age 12 (table 3) also reflected the differential pollen- and seed-cone production. Mean number of microstrobili per pollen cluster varied very little among provenances or from year to year (table 3).

Differences among provenances and among families within provenances were all statistically significant, but over 60% of the variation was associated with the tree-to-tree differences within w.p. families.

Grafts Versus Seedlings

Comparison in conelet production between the grafts in the clone banks and the seedlings in the w.p. progeny plantation is not, strictly speaking, valid because they were neither from the same geographic locations, nor planted at the same site in the same year, receiving the same cultural treatments. However, a comparison of mean production at different ages should be reasonably valid because the numbers of grafts and seedlings investigated were large and they were from similar geographic areas (fig. 1). This comparison is given in table 4. The grafts produced 5 to 10 times more seed cones than the seedlings, and showed similar superiority in pollen-cone production at age 10 and 11. At age 12, however, the seedlings produced as many pollen cones as the grafts. The percent of individuals bearing seed cones or pollen cones was higher in grafts in the clone banks than in seedlings in the w.p. progeny plantation, particularly in the earlier ages.

Table 3.-- Average number of seed cones and pollen clusters, their ratio, and average number of microstrobilus of the 10 provenances which were counted from 1979 (age 10) to 1981 (age 12), provenances arranged from north to south

Provenances				Seed cone			Pollen cluster			Pollen cluster /seed cone			Microstrobilus		
No. Location	Lat.	Long	Elev (m)	10	11	12	10	11	12	10	11	12	10	11	12
31 Frances L., Yukon	61° 10'	129° 20'	884	18	26	3	0	1	2	0	0.1	1.2	19	20	17
66 Stone Mt., B.C.	58° 39'	124° 46'	1173	22	30	18	0	6	23	0	0.3	1.9	21	22	24
27 Pink Mt., B.C.	57° 00'	122° 24'	1113	23	30	32	1	16	53	0.1	0.8	2.3	29	21	26
60 Mt. Lemory, B.C.	55° 33'	122° 33'	732	13	29	27	2	22	82	0.3	1.1	7.0	25	30	27
63 Albreda, B.C.	52° 35'	119° 10'	975	14	46	36	11	114	170	1.8	2.7	12.8	31	28	30
17 Oie L., B.C.	52° 00'	121° 12'	991	10	21	21	6	35	181	1.7	2.9	22.1	27	27	31
14 Wentworth Cr., B.C.	50° 58'	120° 20'	1059	8	30	16	3	34	111	1.0	1.3	18.0	25	28	29
72 Larch Hills, B.C.	50° 42'	119° 11'	777	6	33	20	7	106	189	2.1	3.6	19.2	28	22	32
68 Kananaskis, Alta.	51° 01'	115° 02'	1501	12	26	22	4	55	112	0.7	2.6	6.8	28	28	27
45 Settlers Rd, B.C.	50° 31'	115° 44'	1036	28	82	39	13	199	254	0.8	3.1	11.3	27	32	35
Mean				15	35	24	5	61	123	0.9	1.9	10.5	27	28	29
LSD.05				6	10	8	6	36	39	1.8	1.5	8.2	8	4	6

Table 4.--Comparison in seed- and pollen-cone production between grafted and seedling lodgepole pines

	Seed cone bearing				Pollen cone bearing			
	Graft		Seedlings		Graft		Seedlings	
Age	%[a]	Mean[b]	%[a]	Mean[b]	%[a]	Mean[b]	%[a]	Mean[b]
10	98	113	84	15	68	28	21	5
11	100	237	96	35	89	185	62	61
12	99	128	90	24	80	103	78	123

[a] % of grafts or seedlings bearing seed or pollen cone.
[b] Mean number of conelet or pollen cluster.

Table 5.--Correlation coefficients of mean number of seed cones and pollen clusters, and pollen cluster - seed cone ratio with the latitude, longitude, and elevation of the provenance origin

	Seed cone			Pollen cluster			Ratio		
Origin/age	10	11	12	10	11	12	10	11	12
Latitude	.40	-.19	-.50	-.12	-.37	-.89	-.04	-.03	-.78
Longitude	.23	-.24	-.67	-.32	-.51	-.80	-.10	-.29	-.46
Elevation	-.21	-.19	.09	-.06	-.12	-.07	-.10	-.33	-.26

Notes: 1. Correlations were calculated from provenance means.
2. Age 10 and 11 data are based on 53 provenances; age 12 data are based on 10 provenances.
3. Correlation coefficients significant at 0.05 level are underlined.

eographic Trend

orrelations of cone production with latitude nd longitude of the provenances were relatively igh in the w.p. progeny test (table 5). The orrelation coefficient increased with the age f the trees for pollen-cone production, but changed from positive to negative for seed-cone production. This indicates that provenances from the northwest (i.e., the Yukon) were more precocious but less prolific than those from southeastern British Columbia (i.e., East Kootenay). A similar trend was also evident with the grafts (fig. 3).

Table 6.--Regression analyses with seed cone, pollen cluster, and pollen cluster - seed cone ratio as dependent variables and latitude, longitude and elevation of the provenance origin as independent variables using maximum R^2 method

Number of variables in model	Intercept	Latitude	Longitude	Elevation	R^2
			Seed cone		
One	226.6		-1.68[a]		.45
Two	300.9	1.64[N]	-3.02[N]		.52
Three	466.1	3.30[N]	-4.92[a]	-0.03[N]	.68
			Pollen cluster		
One	1130.9	-18.72[b]			.79
Two	1242.5	-19.35[b]		-0.07[N]	.83
Three	1976.7	-10.13[N]	-9.75[N]	-0.13[N]	.86
			Pollen cluster - seed cone ratio		
One	94.6	-1.56[b]			.61
Two	-69.3	-3.97[b]	2.43[b]		.95
Three	-63.1	-3.90[b]	2.34[b]	-0.00	.95

[N] The regression coefficient not significant.
[a] The regression coefficient significant at 0.05 level.
[b] The regression coefficient significant at 0.01 level.

Table 7.--Age/age correlation (r-value) in seed- and pollen-cone production, and their ratio (pollen cluster:seed cone) estimated by covariance analyses based on the 10 provenances counted from age 10 (1979) to 12 (1981) in w.p. progeny plantation

	Seed cone			Pollen cone			Ratio		
	Age pairs			Age pairs			Age pairs		
Source	10/11	10/12	11/12	10/11	10/12	11/12	10/11	10/12	11/12
Provenance	.62	.39	.66	.95	.92	.87	.85	.88	.74
Families/Prov.	.40	.48	.49	.68	.41	.62	.34	.32	.20
Trees/Fam./Prov.	.57	.46	.56	.56	.30	.53	.31	.17	.20

Regression analyses (table 6) of w.p. progenies revealed that latitude, longitude, and elevation of the provenances together accounted for 68, 86, and 95% of the observed variation for seed-cone production, pollen-cone production, and their ratio respectively, but the effect of elevation was not significant in any case. Geographic trends in seed- and pollen-cone production of grafts in the clone banks were not as obvious (Ying and others 1985b). This can be expected in view of the large within-provenance variation mentioned before.

Age/Age Correlation

High age/age correlation in cone production was observed for both seedlings (table 7) and grafts (table 8). This was true for provenance, family, and individual trees (table 7). These results suggest that a few precocious and prolific clones or seedlings could contribute a large proportion to the genetic composition of the seeds, particularly those harvested from the early years of a seed orchard (Jonsson and other 1976; O'Reilly and others 1982; Todhunter and Po 1982).

Table 8.--Age/age correlation (r-value) in seed cone and pollen-cone production based on clonal means. All correlation coefficients are significant at 0.05 level.

Year (age)	1980	1981	1982	1982
		Seed cone		
1979 (8)	.78	.48	.44	.33
1980 (9)		.71	.66	.52
1981 (10)			.68	.52
1982 (11)				.50
		Pollen cone		
1979 (8)	.46	.81	.41	.43
1980 (9)		.67	.51	.57
1981 (10)			.56	.54
1982 (11)				.80

one Production and Growth

orrelation between cone production and height rowth were all positive at the level of rovenance, family, and individual tree :able 9), indicating that tall trees were also eavy cone producers. In an earlier study, Lee ound an invariable positive correlation between one production and various growth haracteristics in these two clone banks. here is no indication of negative effects of lowering on vegetative growth in either grafts r seedlings of lodgepole pine (Nilsson 1981).

'able 9.-- Correlation of total height at age 13 with seed-cone and pollen-cone production at age 12 in the w.p. progeny plantation, using covariance analysis technique

	Correlation between height and	
ource	Seed cone	Pollen cone
rovenances	.61	.86
amilies/P	.11	.35
rees/F/P	.15	.27

ISCUSSION AND IMPLICATIONS

he superiority of grafts in seed yield and seed eight (table 1) suggests that seeds from a lonal seed orchard will be of better quality han the seeds from natural stands, and thus hould produce better quality seedlings and mprove the nursery recovery factor (the ratio f number of plantable seedlings over number of eeds sown). The nursery recovery factor for eed from clonal seed orchards is predicted to e 0.6 as compared to 0.4 for seed from natural tands (Hewson and others 1984). The low seed-one production by the seedlings (table 4) uggests that clonal orchards would be superior to eedling orchards in terms of seed yield. owever, the lack of pollen-cone production by he grafts during the first 7-8 years (fig. 2) an hinder the rapid advance of a breeding rogram. Field observation indicated more alanced seed- and pollen-cone production by the eedlings at the early ages. Moreover, the esponse of grafts to cone-enhancement treatment n lodgepole pine has not been encouraging Wheeler and others 1982).

t is interesting and useful to compare the eed- and pollen-cone production in the w.p. rogeny plantation at Red Rock with that of a imilar trial at Ange, Sweden (lat. 62° 32'N, ong. 15°42'W, elev. 200 m), which contained rovenances from similar geographic origins Nilsson 1983):

Age (year)		Seed cone		Pollen cone	
ed Rock	Ange	Red Rock	Ange	Red Rock	Ange
)(1979)	15(1978)	15	8	5	26
.(1980)	16(1979)	25	10	61	35
!(1981)	17(1980)	24	13	123	45

Although the Ange plantation was 4 years older, the amount of cone production was only about half of that at Red Rock. Apparently, plantation location has a major impact on cone production.

The pattern of geographic variation observed at Red Rock was also very different from that at Ange: positive correlations between seed-cone production and latitude of the provenance origins were found at Ange (Nilsson 1981), but at Red Rock this correlation was positive only at age 10 (table 5). In other words, at Ange more northern provenances showed more abundant seed-cone production, and this pattern changed little from year to year. At Red Rock, however, this north-south pattern was observed only in 1979, and in 1981 provenances of southern latitude out-produced the northern ones (table 3). No geographic trend in pollen-cone production was apparent at Ange, but a declining northwest to southeast trend was obvious at Red Rock (tables 3, 5, and 6).

Differential adaptation among provenances to respective test sites is apparently the main reason for this disparity in the geographic variation pattern of cone production between Ange and Red Rock. Our experience indicates that vigorous vegetative growth is a prerequisite for abundant cone production in lodgepole pine (Wheeler and others 1982); high correlation between growth and cone production (table 9) suggests that vigorous trees produced more cones (Nilsson 1981). Trees of the Yukon and northern British Columbia seed sources grew poorly in the Red Rock plantation, and at most sites in Interior British Columbia, indicating their poor adaptation (Ying and others 1985a). This apparently also affected their cone production capacity. On the other hand, these northern provenances have been the major sources of lodgepole pine seeds for reforestation and were found to grow well at most sites in Sweden (Lindgren 1983). Poor cone production of the southern provenances at Ange was evidently related to their low vigor. These results suggest that the selection of seed orchard location should follow the similar general guidelines used for seed transfer (Ying and others 1985a, 1985b).

At Red Rock, the prolific cone production of seedlings and grafts originating from southern latitudes (fig. 3, table 3) does not seem to support the common belief that the southward transfer of seed orchards will benefit the cone production (Gansel 1973; Werner 1975; Schmidtling 1983). Until more is known about the effect of site and cultural treatment on cone production of lodgepole pine, the current British Columbia strategy of concentrating seed orchards for the central Interior at Red Rock and for the southern Interior at Vernon appears to be appropriate biologically and economically. The results also suggest that the seed orchard for lodgepole pine from northern British Columbia and the Yukon probably should not be moved to south of latitude 56°.

Both seed- and pollen-cone production showed similar patterns of geographic variation, but the magnitude of differences among provenances was much larger for pollen than for seed cones as reflected in their ratio (table 3). Does this differentiation in sexual ratio among provenances represent the strategy of parental resource allocation, reflecting evolutionary fitness (Doust and Doust 1983)? Or is it environmentally induced due to geographic displacement (i.e., long day length conducive to pollen-cone production as a result of northern displacement) (Larson 1961; Giertych 1967)? Daylength is the prevailing factor affecting cone initiation following geographic transfer. In our case, the maximum northern transfer was about 3° of latitude, equivalent to the maximum increase of about 40 minutes in daylength occurring in June. It is unlikely that this relatively small change in daylength would have such a drastic effect on pollen-cone initiation (Mirov 1956).

The pollen-ovule ratio plays a central role in natural selection associated with sexual reproduction. It is well established that the pollen-ovule ratio increases with the increasing rate of outcrossing (Willson 1979; Doust and Doust 1983); with wind-pollination species, a large quantity of pollen production is probably the most effective way to ensure outcrossing (Willson 1979). That the differential pollen-seed-cone ratio among lodgepole provenances is related to their outcrossing rate appears to be in line with the results of Yeh and Layton (1979). They found the geographic trend of decreasing genetic variability among lodgepole pine populations extending from the southern Interior of British Columbia toward the Yukon Territory. However, it is still not clear why natural selection should favor high outcrossing rates in the southern Interior populations.

Differential seed- and pollen-cone production capacity among clones and geographic sources is of practical significance. First, a few prolific producers (particularly pollen cones) can affect the genetic composition of the seeds from seed orchards (O'Reilly and others 1982). Second, large clonal variation in cone production makes it difficult to achieve the goal of maximizing genetic gain while maintaining the cone production capacity at the time of seed orchard roguing. Third, the risk of pollen contamination increases if seed orchards for different geographic regions are proximally located. In the latter case, pollen contamination could consequently weaken the genetic adaptive capability of seed produced. For example, excessive contamination of the seed orchard for the northern and central Interior of British Columbia by the southern Interior sources can severely impair winter hardiness of progeny seed.

Information reported here is useful in guiding the selection of seed orchard location, projecting seed yield, and alleviating potential problems in lodgepole pine seed orchard management related to pollen contamination and clonal disparity in cone production. However, since the clonal banks and the w.p. progeny plantation are not planted at the same site and not specifically designed to address seed orchard management, questions such as the effect of site and cultural treatments on cone production and seed yield of lodgepole pine grafts and seedlings remain inadequately answered. A study designed to answer the above questions is now in progress. Information generated from this study will further our understanding about the flowering response of lodgepole pine grafts and seedlings under different environments.

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Section 4. Effects of Biological Factors On Seed Production

INFLUENCE OF VERTEBRATES ON CONIFER SEED PRODUCTION

Curtis H. Halvorson

ABSTRACT: Many birds and mammals utilize conifer tree seed but few have feeding strategies or physical capabilities that allow for cone predation prior to seed dispersal.

The American red squirrel is the primary and most effective vertebrate cone predator, although chipmunks also forage in trees for food. Grizzly and black bears use conifer cones in limited fashion. Clark's nutcrackers can have a major impact on cone crops of large-seeded conifers. Jays, crossbills, siskins, and finches are other common bird predators but for most birds our knowledge of their impact is more anecdotal than measured. Low densities and erratic movements suggest most birds can only exert sporadic local pressure on cone crops but could be damaging to high-value seed orchards and production areas.

Red squirrel feeding on ponderosa pine and Douglas-fir cones begins in June and continues through summer, but clipping for storage is timed to seed maturation and starts in early August. Squirrel feeding removed 17 to 100 percent of the annual crop on an island, but a consistent correlation between crop removal and crop production was not found. Seedfall after squirrels' harvest ranged from 15,000 to 172,000 sound seed per acre in good years. Cone clipping by squirrels is often accompanied by loss of branch and terminal buds and first-year conelets. Vegetative parts of conifers may be used when crops fail.

Two highly adapted seed predators, the Clark's nutcracker and the pinyon jay, return some value by being effective seed predators. The cone caches of the most effective predator, the red squirrel, serve as a source of high quality seed for nurseries. The impact of most birds cannot be fully determined from the present, mostly descriptive, literature. And the red squirrel's inconsistent harvest of cone crops appears to be more influenced by weather, seed quality, and the availability of other food rather than simply by cone abundance or squirrel population density.

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INTRODUCTION

Many vertebrates are specialized predators on conifer seeds. Some are more dependent than others. Red squirrels (Tamiasciurus hudsonicus) cache cones in fall, prior to seed dispersal, so that they are assured of a dependable food supply through long boreal winters. The Clark's nutcracker (Nucifraga columbiana) gathers limber pine (Pinus flexilis), whitebark pine (P. albicaulis, and pinyon (P. edulis) seeds into throat pouches during the fall harvest and transports these as far as 14 mi (22 km) (Tomback 1977; Vander Wall and Balda 1977; Lanner and Vander Wall 1980) to ground caches. These become the winter and spring food supply for adult and juvenile nutcrackers. Vertebrate interest in conifers thus produces seed loss if the animal's role is primarily that of a predator, or seed distribution and tree regeneration if the role is primarily that of a disperser. These roles have been studied and will be included in my discussion of the influence of vertebrates on seed production.

Man's interest in seed includes an economic dependency that seeks to enhance seed production to produce wood commodities. We are interested in seed losses and have catalogued vertebrate influences and their control in the past. By 1915, according to Pank's (1974) bibliography on animals and tree regeneration, there were eight government and forestry publications discussing reforestation and vertebrate agent problems. Several hundred reports and numerous conferences have followed (Smith and Aldous 1947; Tevis 1953; Radwan 1963; Black 1969, 1974; Janzen 1971; Pank 1974). Most focus on post-dispersal seed loss and subsequent stand establishment, damage, and protection. The usual scenario is: cones open releasing seeds, which are gathered and consumed by rodents.

I will confine my review to those animals that reach the seed before it leaves the tree. This is predispersal impact and is far less quantified than that for shed seed. Those animals that have specialized adaptations for harvesting predispersed seed are primary influences. There are secondary influences on seed production--bears stripping cambium, porcupines (Erethizon dorsatum) girdling conifers--but I will confine descriptions to the primary agents. I will describe these adaptations and their effects and implications on seed reproduction. The birds and mammals discussed herein (table 1) are mostly residents

Table 1.--Vertebrates of the Inland Mountain West that use conifer seed prior to seed dispersal (Table modified from Smith and Balda 1979)

Taxonomic Group	Genera of trees	Method of using seed	References
BIRDS:			
Family:Picidae			
Hairy Woodpecker Picoides villosus	Pinus	Extracted seed from closed and open cones are eaten by adults and juveniles	Ligon 1973, Smith and Balda 1979; Stallc 1968, 1969; Tomback 1977
White-headed woodpecker Picoides albolarvatus	Pinus	Extracted seed from closed and open cones are eaten by adults and juveniles	Curtis 1948; Ligon 1973; Smith and Balda 1979; Tevis 1953; Tomback 1977
Family:Corvidae			
Gray Jay (questionable) Perisoreus canadensis	Abies, Picea	"May extract seeds from open cones or retrieve from ground to eat and store as boli"	Smith and Balda 1979 list without eviden see Dow 1965 for feeding test; Turcek and Kelso 1968 list European jay P. infaustus
Steller's Jay Cyanocitta stelleri	Pinus	Cache seed from open cones to feed adults	Benkman et al. 1984; Curtis 1948; Smith and Balda 1979; Tevis 1953
Pinyon Jay Gymnorhinus cyanocephalus	Pinus	Cache seed extracted from closed and open cones to feed adults and young	Ligon 1978; Smith and Balda 1979; Turcek and Kelso 1968
Clark's Nutcracker Nucifraga columbiana	Pinus, Pseudotsuga	Cache seed extracted from closed and open cones to feed adults and young	Benkman et al. 1984; Curtis 1948; Guintol and Mewaldt 1978; Lanner and Vanderwall 1980; Smith and Balda 1979; Tomback 19 1980, 1981, 1982; Vanderwall et al. 19
Black-billed Magpie Pica pica	Pinus	Cache seed from open cones and ground to feed adults	Smith and Balda 1979 (Vanderwall and Balda, unpublished)
Family:Paridae			
Black-capped Chickadee Parus atricapillus	Abies, Picea, Pseudotsuga Pinus	Cache seeds from open cones and ground to feed adults	Bent 1946; Curtis 1948
Mountain Chickadee Parus gambeli	Abies, Picea, Pseudotsuga Pinus	Cache seeds from open cones and ground to feed adults	Benkman et al. 1984; Haftorn 1974; Smith and Balda 1979; Stallcup 1968, 1969; Te 1953; Tomback 1977
Boreal Chickadee Parus hudsonicus	Abies, Picea, Pseudotsuga	Cache seeds from open cones and ground to feed adults	Haftorn 1974; Smith and Balda 1979
Family:Sittidae			
Red-breasted Nuthatch Sitta canadensis	Abies, Picea, Pinus, Pseudotsuga, Tsuga	Seeds from open cones cached and eaten by adults	Benkman et al. 1984; Curtis 1948; Smith and Balda 1979; Stallcup 1969; Tevis 19
White-breasted Nuthatch Sitta carolinensis	Pinus	Uses and makes cache of seeds and finds seed on ground	Curtis 1948; Smith and Balda 1979; Stallcup 1969; Tevis 1953; Tomback 197
Pygmy Nuthatch Sitta pygmaea	Abies, Picea, Pseudotsuga, Pinus	Seeds from open cones cached and eaten by adults	Ligon 1973; Smith and Balda 1979; Stallcu 1969
Family:Fringillidae			
House Finch Carpodacus mexicanus	Pinus	Feeding on opening cones and seed fallen on ground	Curtis 1948
Red Crossbill, White-winged Crossbill Loxia curvirostra, L. leucoptera	Abies, Larix, Picea, Pinus Pseudotsuga, Tsuga	Seeds from closed and open cones fed to adults and young	Bock and Lepthien 1976; Curtis 1948; Kemper 1959; Ligon 1973; Newton 1973; Smith and Balda 1979; Stallcup 1969; Stickney (1966 pers. comm.); Tomback 19
Common Redpoll Carduelis flammea	Pinus	Feeding on opening cones	Bent 1968; Curtis 1948; Newton 1973
Pine Siskin Carduelis spinus	Abies, Larix, Picea, Pinus Pseudotsuga, Tsuga	Seeds from open cones and the ground fed to young adults	Benkman (pers. comm.); Bent 1968; Smith and Balda 1979
MAMMALS			
Order:Rodentia			
Red Squirrel Tamiasciurus hudsonicus	Abies, Larix, Picea, Pinus, Pseudotsuga, Tsuga	Cache and feed from whole closed cones	Curtis 1948; Duncan 1954; Finley 1969; Gurnell 1984; Kemp and Keith 1970; Schm and Shearer 1971; Shaw 1936; Smith 1970 Smith and Balda 1979
Chipmunk Eutamius	Abies, Larix, Picea, Pinus, Pseudotsuga, Tsuga	Cache and eat seeds from closed or open cones	Benkman et al. 1984; Broadbrooks 1958; Schmitz (1966 pers. comm.); Tomback 197 1981
Golden-mantled Ground Squirrel Spermophilus lateralis	Pinus	Forage for single seeds	Benkman et al. 1984; Smith and Balda 1979 Tomback 1977, 1981
Order:Carnivora			
Grizzly and Black Bear Ursus arctos; U. americanus	Pinus albicaulis	Major fall food from squirrel caches; some tree climbing by black bear	Kendall 1983; Mealey 1980; Murie 1981; Tisch 1961

of the geographic area prescribed for this symposium, the Inland Mountain West, lying between the east slopes of the Cascades and the western edge of the mixed-grass prairie in Alberta and Montana. Important knowledge of some bird species has come from adjacent areas; these and pertinent foreign literature are included where applicable.

Background References

Background information on animals and their use of tree mast has been reviewed by Janzen (1969, 1971-insects, birds, and mammals), Smith and Balda (1979-competition between animals for conifer seed), and Smith and Reichmann (1984-food caching behavior). Boreal forest birds, their Holarctic distribution and adaptations to coniferous forests, have been covered by Udvardy (1969), with emphasis on the Northern Rocky Mountains. The Corvidae (crows and jays), have special behavioral adaptations for food movement and storage, particularly conifer seeds, and these habits are reviewed by Turcek and Kelso (1968) for 22 European and North American species. Tree squirrels are the only mammals that relate importantly to tree mast. Gurnell (1983) has provided a major review of Palearctic and Nearctic tree squirrel behaviors and population responses to seed crops; Heaney (1984) included tree squirrels in summarizing climatic and latitudinal relationships to life histories of the Sciuridae. The nature of red squirrel cone caching, energy supplies, and some forest regeneration implications are described by Finley (1969). The evolutionary history of squirrels is thoroughly discussed by Black (1972), Emry and Thorington (1984), and Hafner (1984); Brodkorb (1971) describes the fossil record on birds. These reviews are useful references for readers seeking perspective on vertebrates and predispersed seed crops.

Some History

Modern conifers were geologically well-established in the Cenozoic Era about 70 million years ago (Egler (1977). Ancestors of our present birds and squirrels appeared much later, in the mid-Miocene, about 18 million years before present (ybp; Brodkorb 1971, Black 1972, Hafner 1984); by the Pleistocene, modern forms used conifer seeds much as we see them now. The adaptations between vertebrates and conifer seeds in the Inland Mountain West were already well established genetically when the late Pleistocene glacial ice sheets excluded most forests from the Northern Rocky Mountains, beginning 42000 ybp, and were maintained after re-establishment of forests as recently as 12000 or fewer years ago in some areas (Heusser 1969).

The adaptive behaviors of animals of the montane West stem from the seasonality of the taiga--the extremes in seasonal temperatures and moisture. Most birds migrate altitudinally at least, or latitudinally at most, in response to annual food shortages. Invertebrates disappear, most seeds and berries fall, plants dry and go dormant. A few, chiefly the corvids (crows, jays, nutcrackers), store food over winter whereas nuthatches (Sitta spp.) and chickadees (Parus spp.) do so only for days or weeks (Udvardy 1969). Red squirrels cache and defend their winter supply of cones (Smith 1968; Gurnell 1983) but chipmunks (Eutamias spp.) take their seed hoards to bed, packing several thousand at a time under and around their underground nests (Broadbrooks 1958). Bears (Ursus arctos, U. americanus) also take their food supplies into hibernation but as energy already assimilated as fat tissue. Man's economic concerns about vertebrate use of seed seldom reflect on the fact that animal use of seed is an evolutionary phenomenon enabling species to occur in certain geographic areas. It is difficult for us to comprehend the pace of adjustments that occurred during the coevolution of birds, mammals, and trees. Animals must adapt to external conditions of food abundance and scarcity or die, while man can create and, to large extent control, his own food supply and living environment.

Interactions: Mutualism and Defense

In recent years there has been renewed interest in vertebrate-seed relationships that goes beyond the economic aspects of seed-eating related to losses in tree regeneration. This interest has looked at seeds and their vertebrate predators as biological interactions between two organisms--the plant seeking effective mechanisms for reproducing and the vertebrate using the plant for survival. Negative interactions as coevolved defensive mechanisms were initially emphasized in this "new look" (Smith 1968, 1981; Janzen 1969, 1971; Elliot 1974). Janzen (1971) considered that trees are not entirely helpless and over time have envolved mechanisms to defend themselves. These mechanisms include satiating the predators and minimizing the feeding intensity (Janzen 1971). The entire seed crop could ripen synchronously and overwhelm the harvesting ability of predators, as Benkman and others (1984) concluded for southwestern white pine (Pinus strobiformis) and the red squirrels. If seed crop abundance occurs only at long intervals, and predator peaks lag the seed crop peaks, then predators whose population build-ups are related to seed crop abundance have reduced populations and less predation capability.

Another defense mechanism may be present in lodgepole pine (Pinus contorta). Cone serotiny and smaller, fewer seeds in the harder serotinous cones have been theorized as tree defenses against red squirrels (Elliott 1974; Smith and Balda 1979). The squirrels, in turn, develop heavier jaw musculature, according to Smith (1970, 1981). But if hard nuts and cones predate the origin of squirrels, a suggestion by Emry and Thorington (1984), then plants might first have developed some of their

defenses against geologically older factors such as insects or fire.

Odum recently (1985) advised against population ecology focusing on the negative interactions--competition and predation--and predicted more study of positiveness--cooperation and mutualism. Mutualism requires that the association between different organisms increase the fitness of both, not just one. The seed dispersal activities of fruit-eating birds and mammals examined by Krefting and Roe (1949) have been recognized as mutualism, as have pollinating insect interactions reviewed by Owen (1980). An argument has been made by Owen and Wiegert (1981) for the stimulating effects of grazer saliva and feeding on grasses. Owen (1980) further theorizes that removal of plant growing points, apical shoots and buds, is favorable to the plant because it induces branching, to the extent that a plant is better supported, photosynthetic parts are more favorably exposed, and seed production is increased by profuse branching. Although he does not mention squirrel clipping of terminal buds, it is an activity I have observed and will allude to later, as a factor in ponderosa pine (Pinus ponderosa) branch morphology. A recent paper by Tomback (1982) portrays this increasing interest in mutually beneficial coevolved relationships and provides substantial evidence that the seed dispersal activities of the Clark's nutcracker are more effective than that of rodents and other animal agents (see also Hutchins and Lanner 1982). The nutcracker caches whitebark pine seed in conditions particularly suited for germination and seedling survival and most likely to provide the best recruitment to the pine population. Favorable aspects of nutcracker caching include moving this heavy wingless seed away from under the immediate tree canopy, often into pioneering habitats such as burns, thereby reducing concentrations for rodent predators. In Utah a high elevation burn is being restocked with limber pine by the seed caching activity of Clark's nutcracker (Lanner and Vander Wall 1980). Similar beneficial relationships have been suggested between the wingless pinyon pine (Pinus edulis) seed and the pinyon jay (Gymnorhinus cyanocephalus) (Ligon 1978) but hard evidence to date shows the benefit only to the bird.

SEED AS FOOD

Seeds are a particularly efficient food resource for animals. They are a sessile prey that periodically occurs in large abundance, are durable to store, and have a dormancy that improves storage survival, particularly in the cooler temperate zones where caching behavior among birds and mammals seems more common (Smith and Reichman 1984). Viable conifer seeds, the condition animals normally select for, are uniform in size and have a clumped distribution when in the cone, making them highly visible and accessible to those animals having the physical abilities and feeding strategies adapted to using this resource in the tree. Conifer seeds have higher energy values when compared to seeds of most angiosperms; deciduous tree exceptions being shagbark hickory nuts (Carya ovata) and black walnut (Juglans nigra) whose 6302 and 7221 cal/g dry weight (dw) of endosperm and embryo (Smith 1970) is in the mean range (6781± 760 cal/gm dw) of 19 conifer species reviewed by Grodzinski and Sawicka-Kapusta (1970). Smith (1968) determined the average caloric value of eight conifer species to be about 7000 cal/g dw; ponderosa pine having the highest at 7558 (SD 132) cal/g dw and lodgepole pine the lowest at 6827 (SD 152) cal/g dw. The average value of 400 plant species seeds tested by Golley (1961) was 5065 (CV 219) g cal/g dw, although he included seed head and coat material. In conifer seeds the shell can constitute about 20 percent of a seed's caloric value (Smith 1970). The superior nutritive quality of conifer seeds comes from their high lipid content (Smith 1970) and lipids have the highest caloric content (about 9000 cal/g dw) of basic nutrition elements. Proteins average about 5000 and carbohydrates about 4000 cal/g dw (Smith and Follmer 1972). Smith (1970) recorded the digestive efficiency of two red squirrels at 90 percent on nut kernels and reported the digestive ability was about in proportion to the caloric value or lipid content. Fat is the principal food storage form in conifer seed (Rediske 1961) and a most durable form in cool storage such as a squirrel midden.

The importance of conifer seeds in the diets of their animal users is incompletely known. It has been explored for the red squirrel by Smith (1968) and Finley (1969) in speculative discourse, and for the Clark's nutcracker by Tomback (1982) more precisely. It is difficult to measure the total energy needs, use, and contribution of conifer seeds to free-living birds or squirrels and at present the relationships can only be crudely estimated. Anyone who has watched a red squirrel in daily activities can see they are extremely energetic creatures. Their basal metabolic rate is 1.76 times that expected for an animal its size (Irving and others 1955). The daily energy consumption for an adult male red squirrel in summer averaged 117 kg cal and for a lactating female 322 kg cal (Smith 1968). Five half-grown juveniles consumed about 25 percent (80.5 kg cal) of their mother's daily requirement during nesting. Smith calculated that a squirrel's territory contained nearly the average total estimated food energy required (42,700 kg cal-Finley 1969) by a squirrel. These figures are to be accepted with fair caution, as mentioned earlier. On the basis of a squirrel perhaps getting half its subsistence from other foods such as fungi, fruit, and flower heads, Finley (1969) provides estimates of the amount of seed needed from five conifer species for the other half of a squirrel's energy needs (table 2).

able 2.--Estimated amounts[1] of seed needed to provide 21,350 kg cal, half f the annual energy requirement of an adult Tamiasciurus

	Douglas-fir	Engelmann spruce	Blue spruce	Ponderosa pine	Lodgepole pine
housand fresh whole seeds	400	1200	910	170	1300
g of fresh whole seeds	4.4	3.9	3.9	5.2	5.8
g of dry seed kernels	3.0	3.0	3.0	2.8	3.1
umber of cones	9200	--	--	2400	62,000
ushels of cones	13	17	8.6	8.7	24
umber of good seed trees	8.5	14	17	6	47
cres of forest	3.2	2.0	1.7	0.8	4.1

[1]The values in this table are internally inconsistent because they are derived from several independent sources. (From Finley 1969). Figures represent a broad linking of averages and areas to derive relations between quantities of seed, cones, trees, and area. Figures could be refined considerably through further study.

The Clark's nutcrackers studied by Tomback (1982) in the eastern Sierra Nevada recovered stored whitebark pine seed from about April to July and the total energy requirements were estimated at 16000-25500 kJ (min-max) or 133 to 213 kJ per day. These caloric requirements convert to 50 to 84 seeds per day, amounts a nutcracker can readily carry in its throat pouch. The red squirrel and Clark's nutcracker energy requirements have been more intensively evaluated than any other species I will discuss. Because conifer cone crops fluctuate considerably, the effects of the varying, highly nutritious food supply will be discussed later.

PREDATOR OR SEED DISPERSAL AGENT

Predispersal seed removal by vertebrates represents an interception in the normal cycle of a tree. A superficial judgment would class the act as predation and the agent as a predator. A distinction exists between seed predators and seed dispersers (Smith and Aldous 1947; Turcek and Kelso 1968); predators being those whose seed use results in seed destruction, as opposed to the seed dissemination effect of dispersers. Janzen (1971) judges the two roles according to the precision with which seed processing (i.e., completeness of assimilation) occurs, and whether the agent seeks the fruit or the seed. After passage through the gut of six bird and four mammal species, the fruit of 25 different woody plant species mostly showed either no viability loss or improved germination (Krefting and Roe 1949). Such processing inefficiency would class the vertebrate consumers as dispersal agents. Krefting and Roe (1949) also found that the dispersal role of many animals was enhanced because passage through the gut helped overcome seed-coat dormancy. In most cases the desired food item was fleshy fruit material rather than seed. With conifer cones, the seed is the sought-after food material and most vertebrate agents that gather conifer seed act primarily as predators.

Of the 44 mammals and 37 bird species listed by Smith and Aldous (1947) as North American conifer seed eaters, the red squirrel can be considered the primary predator because of its efficiency in cutting cones from trees (Tevis (1953; Smith 1970; Shearer and Schmidt 1970; Schmidt and Shearer 1971; Harvey and others 1980; Gurnell 1983; C. H. Halvorson unpublished), and deeply burying these under damp conditions that preclude seed release (Shaw 1936; Finley 1969). Other mammalian gatherers and eaters of predispersed seed are given lesser attention because either they do not forage on commercially important conifers, or they eat seed but also cache it in clusters that often are not recovered, and later germinate. Grizzly and black bears are in the first category because the large seeds of the non-commercial whitebark pine are eagerly sought (Tisch 1961; Mealey 1980; Kendall 1983). Chipmunks and golden-mantled ground squirrels (Spermophilus lateralis) eat but also pouch seeds and cache them in shallow pits, failing to recover some portions of those (Tevis 1952, 1953; Broadbrooks 1958; West 1968). Red squirrels do not have cheek pouches, and thus store whole cones that do not germinate, therefore their storage act is not that of dispersal.

Most notable in the role of a dispersing agent are some members of the crow family (Corvidae), chiefly the pinyon jay and the Clark's nutcracker (table 1), who distribute seeds away from the trees and cache more than they recover. Of course they also consume seed but when the gathering is done in years of seed abundance the birds bury more seed than they consume (Tomback 1982). The other bird families (table 1) recognized as conifer seed gathers and feeders from cones are finch-types (Fringillidae), nuthatches (Sittidae), chickadees (Paridae), and a few woodpeckers (Picidae). Some of these groups may cache seeds for short periods of days or weeks, as with chickadees and nuthatches (Kilham 1974; Sherry 1984), but for the most part the families other than corvids can be considered predators on predispersed seed.

SPECIES THAT FORAGE ON PREDISPERSED SEED

The manner in which vertebrates forage on predispersed seed has been described by Smith and Balda (1979) as: removing the entire cones and caching (squirrels); extracting seed from green or ripe closed cones, with some birds performing storage (woodpeckers, crossbills, jays); searching and extracting seed from opening or opened cones (chickadees, nuthatches, small finches).

The physical and behavioral adaptations to these foraging methods are the subjects of this section. None of the species discussed (table 1) are such extreme specialists that they subsists only on conifer seeds. The sporadic nature of seed crops would not have allowed survival. The crossbills (Loxia spp.) are most closely linked to conifer seeds, in feeding, reproduction and movement, but in common with the other birds listed, they also utilize buds and insects. Fungi are important to rodents (McKeever 1964; Smith 1968; Sanders 1983; personal observation) and bears eat carrion and forage on herbaceous vegetation, roots and berries (Tisch 1961; Mealey 1980; Murie 1981). Despite certain foods being especially sought, usually large-seeded pines, none of the birds or mammals have distributions confined to the range of any one tree species.

I have tried to limit the vertebrate list (table 1) to those whose primary feeding behavior is that of taking cones or seed from the tree. That does not preclude their also foraging on shed seed or clipped cones as secondary efforts. The five bird and two mammal families that forage on predispersed seed include at least 22 species of vertebrates (table 1). All those shown occur across the northern Rocky Mountains. The listing is based on Smith and Balda (1979) but omits species out of the range in question, such as the scrub and gray-breasted jays (Aphelocoma coerulescens, A. ultramarina), plain titmouse (Parus inornatus), and shrews (Soricidae) and mice (Cricetidae) that only use dispersed seed. Added are two bears--the grizzly and black; and three birds--the black-capped chickadee (Parus atricapillus), house finch (Carpodacus mexicanus), and common redpoll (Carduelis flammea). The additions are based on references not available or not included by Smith and Balda (1979). To the bird listings could be added Williamson's sapsucker (Sphyrapicus thyroideus), reported by Tomback (1977) to occasionally take whitebark and Jeffrey pine seed (Pinus jeffreyi) from cones, or forage on Arizona limber and southwestern white pine cones during opening (Benkman and others 1984). The pine grosbeak (Pinicola enucleator) was observed by Tomback (1977) as a subalpine transient in the Sierra Nevada, taking whitebark and Jeffrey pine seed from cones. This grosbeak has been recorded primarily as a bud, fruit, and catkin feeder (Bent 1968; Newton 1973). My inclusion of the gray jay (Perisoreus canadensis) and black-billed magpie (Pica pica) is based on Smith and Balda (1979) although the former species remains undocumented as a conifer seed feeder. The authors cite unpublished data that the magpie harvests pinyon pine in Utah where the Steller's jay (Cyanocitta stelleri) is absent. In feeding tests (Dow 1965) that deliberately exposed gray jays to conifer cones (Abies lasiocarpa, Psuedotsuga menziesii) the birds showed a weak but negative interest in cones compared to strong search effort on bark and rotted logs. The test timing (March and April) would have been at the extreme end of seed dispersal time (Schopmeyer 1974) for these conifers in the western ends of their range (British Columbia Cascades, Vancouver) and might have contained unsound seed, normally the last to shed. When later tested with lodgepole pine that had seeds visible in partly opened cones the birds pecked but did not attempt to extract them, despite the birds being without food several hours prior (Dow 1965). The European jay (Perisoreus infaustus) is cited in many accounts listed in Turcek and Kelso (1968:282) as taking and caching Siberian stone pine (Pinus siberica), Norway spruce (Picea abies) and other conifer seeds. Further study of the gray jay relationship with conifer seeds is desirable because it is a Nearctic winter resident throughout its range in the boreal forest (Udvardy 1969; Welty 1975).

In the inland West all species in table 1 are year-long residents in a portion of those states bordering Canada and southward. It is characteristic of resident species of the taiga or northern coniferous forest that they are mostly seed-and nut-eaters and insect feeders (Welty 1975). In Montana only the white-headed woodpecker (Picoides albolarvatus) is not a resident. However, many of the birds show altitudinal migratory behavior after breeding, moving between forest communities with the onset of harsh weather, or latitudinally from one region to another, sometimes showing irruptive behavior in response to food scarcity. True migratory birds of our northern coniferous forests outnumber the residents. Udvardy (1969) attributes this paucity of complete adaptation to the sharp seasonal changes and relatively recent and interrupted expansion of boreal forests during interglacial periods. The adaptations birds especially have made is to migrate, to shift their food habits between summer and winter, and to prolong food availability by storing it. Mammals also show these adaptations, but rather than migrate some are dormant during winter.

The species descriptions that follow are patterned after Smith and Balda's (1979) succinct presentation, which should be read for additional insight on competition between seed eaters.

Birds

Woodpeckers.--Only recently was the hairy woodpecker (Picoides villosus) described feeding on intact conifer cones in the tree. However, an early record from 1928 is cited by Bent (1939) that seed, mostly conifer, averaged 12 percent in the diet (not identified as being volume or occurrence) of a humid-forest west coast subspecies of the hairy woodpecker (P.v. harrisi). The origin of the seed was not disclosed and could have been from ground foraging which is out-of-character for this bird. Stallcup (1968, 1969) provided the first accounts after observing hairy woodpeckers perched and feeding on pine cone clusters.

Attacking only the upper surface of ponderosa pine cones with their bill, they hammered and pecked, sometimes twisting bracts loose from the seeds which were also pecked open instead of cracked as finches do. The feeding occupied about 65 percent of their foraging time from mid-October through February in this Colorado study. Early spring foraging on ponderosa pine was also observed by Ligon (1973), and occasional feeding on whitebark and Jeffrey pine occurs in the Sierra Nevada (Tomback 1977).

The white-headed woodpecker was recognized as a pine seed feeder in 1911 (Bent 1939). All reports (Curtis 1948; Tevis 1953; Ligon 1973; Tomback 1977) refer to feeding on the large seeded species: ponderosa pine, Jeffrey pine, sugar pine (P. lambertiana), and whitebark pine. Spring (April) foraging on ponderosa pine cones in Idaho consisted of a few birds foraging steadily through open second-growth pine, chipping cones open for seed while clinging to them. In early August the birds attacked the hard green cones and extracted unripe seed (Ligon 1973). Three females that Ligon collected in October had their stomachs 60-70 percent filled with pine seeds. Tevis (1953) describes late-August feeding on California sugar pine cones two weeks prior to ripening. Groups of four to six birds "slashed open every cone on which they alighted and ate the seeds, leaving deep vertical trenches....." He reported 34 percent (559) cones destroyed. They concentrated on certain trees, thus one pine lost 85 percent (252) of its cones. White-headed woodpeckers reach the northern and eastern limits of their range in Idaho (Burleigh 1972) and are not common in Washington, although they are residents there also (Jewett and others, 1953). The Williamson's sapsucker may be a conifer cone feeder (Tomback 1977; Benkman and others 1984), but this is not substantiated enough to assess the importance to regeneration. Of the woodpeckers listed, the white-headed presently appears to be the species most interested in cones and able to damage them in quantity.

Jays.--Despite not having real evidence that the gray jay is a conifer seed consumer, the "Whiskey Jack" is a ubiquitous and territorial inhabitant of northern coniferous forest. Yet their use of plant material as food is hardly known (Rutter 1969). They are well-known omnivores especially attracted to meat and camp scraps. Their particular attribute is the ability to store food amidst conifer needles and in and on tree trunks and branches (Dow 1965). This storage is achieved by orally manipulating food until it is completely coated with thick saliva to become a mucous pellet or bolus. The saliva allows adhesion to a substrate (Dow 1965) and would seem ideally suited for caching seed, but there are no records to that effect. Captive jays were unable to open sunflower seeds and gray jays seemed committed to a single bill-shoving motion when burying (in captivity only) or storing food. The hammering motion that is used by other seed feeding corvids to store or extract conifer seeds was never observed by Dow (1965). Smith and Balda's (1979) inclusion of the gray jay as a conifer seed eater seems unwarranted at present and I have included it only because of its congener, the European jay, a known seed user (Turcek and Kelso 1968).

Three other jays, Steller's, pinyon, and Clark's nutcracker, share typical jay characteristics of strong bills and feet, social system, and a food storage instinct. The Steller's jay remains the least studied of the three. Tevis (1953) described the Steller's foraging in sugar pine when cones opened, "launching" from a branch to strike a cone and dislodge seed which was seized in mid-air, carried to a limb, and the kernel pounded open. This jay travels in raucous groups, concentrating on trees with opening cones. Only Smith and Balda (1979) mention storage, and large flocking movements do not appear in the reviews previously cited. The Steller's jay seems to be an inconsequential seed predator from knowledge presently available.

Pinyon jays live and feed in close association with pinyon pine - juniper (Juniperus spp.) communities but also occur with ponderosa pine, a seed readily accepted in lieu of the infrequent pinyon seed crops (Bent 1946; Balda and others 1972; Ligon 1978; Schopmeyer 1974). They readily extract conifer seed (table 1) from green or opening cones by hammering in jay fashion; they bury seed clusters in pockets, and practice communal caching, usually on open, warm-aspect slopes. From 30-50 seeds at a time can be transported in a distensible esophagus. The food is used later in winter and as food for new hatchlings in early spring (Ligon 1978). These strong fliers search widely for food, up to 13 miles (21 km) daily (Balda and others 1972). These behavioral characteristics are quite similar to those in the Clark's nutcracker, but the pinyon jay shows a unique physiological adaptation to cone abundance that is shared with the red crossbill (Loxia curvirostra), a bird more distinctly associated with montane and boreal forest. Pinyon jays can be stimulated to breeding readiness and actual breeding by the presence of an abundant pine crop. Thus, Ligon (1978) found breeding readiness (gonadal development) in early December, February breeding after a large pinyon seed crop, and August breeding in the presence of a large maturing seed crop that was used to feed young. He reported this only for southwestern New Mexico and similar behavior in northern parts of the jay's range is unknown. Pinyon seed volume in stomachs reached 95 percent in December to 50 percent in May as birds continued to use caches, then tapered to 20 percent in summer until new seed became available.

The Clark's nutcracker is the most thoroughly studied of the predispersal seed-eating jays, partly because its eruptive migrations are

well-known (Davis and Williams 1964; Turcek and Kelso 1968; Bock and Lepthien 1976) and its seed storage behavior has been thoroughly documented, but only in the last 15 years (table 1). In contrast, its Palearctic counterpart, the Eurasian Nutcracker (Nucifraga caryocatactes), has a long record of observation on feeding behavior and population migration (Formosof 1933; Turcek and Kelso 1968) in conjunction with fluctuations in its primary food, the Siberian stone pine (P. cembra). The Clark's nutcracker is superbly adapted to feeding on conifer seeds year round and, like the Eurasian nutcracker, possesses a sublingual throat pouch (Bock and others 1973) to store and transport food. This is more highly specialized than the pinyon jay's expandable esophagus and holds about 20 ml (125 limber pine) of seed (Lanner and Vander Wall 1980). The nutcracker depends heavily on whitebark, limber, and ponderosa pine (and related Jeffrey) pine extensively (Curtis 1948; Tomback 1977, 1981; Lanner and Vander Wall 1980) but readily takes Douglas-fir (Pseudotsuga menziesii) in the absence of the larger-seeded species (Giuntoli and Mewaldt 1978; Fisher and Myres 1980; Vander Wall and others 1981). The typical foraging pattern was first delineated by Tomback (1977) in the Sierra Nevada. The adult birds began harvest from unripe closed whitebark pine cones in mid-July. Seeds were exposed by forcefully repeated stabs to loosen and tear off scales. Soft seeds were removed piecemeal and eaten or moved into the sublingual pouch by a backward toss of the head. Hardened ripe seeds were extracted whole at a rate of about one per 7 sec. after scales were twisted and broken off. Seed soundness was detected by "bill-clicking" or rattling the seed within the mandibles; unsound seed being discarded. Pouch contents averaged 77 whitebark seeds. Storage occurred initially in late August in high elevation subalpine habitat but flights were also made at this time to lower elevations in the Jeffrey and ponderosa pine zones, to store whitebark seed for winter use, and also to "test" lower elevation seed. Harvest and storage of subalpine whitebark seed ended about mid-October but many birds had already moved to lower elevation wintering areas to harvest ponderosa or Jeffrey pine. Because whitebark pine cones are indehiscent, the birds continued to forage on any available in winter. The seed recovery period at lower elevations was from late December to late March with young being fed cached seed starting very early in spring. Upon returning to higher elevations in early summer the birds used subalpine caches. Tomback (1977) concluded that these altitudinal movement patterns were comparable to those reported from Montana (Giuntoli and Mewaldt 1978). The onset of harvest on limber pine in Utah was also similar (Lanner and Vander Wall 1980).

From a full pouch of whitebark pine seed a nutcracker will successively distribute 3.7 ± 2.9 seed per cache, burying them at a mean depth of 2.0 ± 0.8 cm (Tomback 1982); caches of limber pine were similar (4.2 ± 3.1 seeds per cache at 2-3 cm depth (Lanner and Vander Wall 1980). Seed cache recovery apparently relies heavily on memory, supplemented by visual cues (see Tomback 1980). Eurasian nutcrackers can find stored seed under snow less than 2 m deep (in Tomback 1980). Olfactory detection was recently tested in another corvid, the magpie, and reported to show at least close distance effectiveness (less than 1 m) on cod liver oil (Buitron and Nuechterlein 1985). Corvid olfactory bulbs are quite small compared to birds with known olfactory capabilities.

The seed use pattern of Clark's nutcracker (and pinyon jay) is to store seed when it is seasonally plentiful (fall), with subsequent recovery when it is scarce but needed by nestlings (winter-spring). Conifer seed was the most important year-long food in 426 nutcracker stomachs examined from Montana (Giuntoli and Mewaldt 1978). Average importance of weighted samples from four years showed conifer seeds constituted 83 percent of stomach volume balance but occurred 59 percent of the time, mostly in summer. Ponderosa seed volume and frequency (52 percent, 80 percent respectively) were greater than whitebark (19 percent, 42 percent respectively) in this Montana study. The collection elevations between 3280-8500 ft (1000-2500 m) spanned the distribution of the pines in western Montana. Seed consumption was strongly influenced by availability. A bumper Douglas-fir seed crop in 1946 provided most of the fall-to-spring diet in the presence of only a moderate ponderosa cone crop. In 1948, a very heavy ponderosa crop was reflected by only those seeds occurring in stomachs between September 1948 through last samples from May 1949; this occurring with "moderate crops" of whitebark and fir present.

The black-billed magpie (Pica pica) is not cited as a conifer seed eater except by Smith and Balda (1979) who refer to unpublished data from Utah (Vander Wall and Balda) that the magpies take pinyon pine seed in the absence of Steller's jays. The magpie in Europe stores angiosperm nuts as does the yellow-billed magpie (P. nuttali) in California (Turcek and Kelso 1968).

Chickadees.--Chickadees (Parus spp.) are small tame birds resident to the coniferous forest of Canada and the U.S. They forage industriously on tree trunks, branches, foliage, and the ground, using their short, strong acute bills to extract and store arthropods, spiders, insects, and seed in bark crevices (Haftorn 1974). In searching open conifer cones they typically cling to the underside or hang upside down, grasping seed wings and tugging the kernel from between the cones scales (Bent 1946). All conifer species are used, including the larger seeds like ponderosa, limber, whitebark, and Jeffrey pine (Curtis 1948; Tomback 1977; Benkman and others 1984). The

black-capped and the mountain (P. gambeli) chickadee occur with conifer distribution in the West Coast Corderilleran and Rocky Mountain Ranges. The boreal chickadee (P. hudsonicus) is most common in Canada and Alaska but dips down into Washington and Montana. At least short-term (24 hour) memory has been demonstrated for the black-capped chickadee in relocating stored seed (Sherry 1984) and food storage allows prolonged predation. Although no evaluation of impact occurs in the literature, the chickadee, like other small seed-foragers (nuthatches, small finches) cannot engage closed cones and must concentrate seed gathering for the brief period between cone opening and seed shedding. It therefore seems unlikely that chickadees have much impact on predispersed conifer seed.

Nuthatches.--The nuthatches (Sitta spp.) (table 1) are behaviorally related to chickadees in many seed foraging mannerisms. Although the nuthatches are particularly adept at working up and down vertical surfaces in their search for insects they also mount open cones from all angles to pull seed out, eating it or storing by poking or hammering them under bark or into crevices (Bent 1948; Ligon 1968; Kilham 1974; Smith and Balda 1979). Species of both families search assiduously among foliage and branches but nuthatches feed on the ground less than chickadees and only occasionally probe fallen cones (Stallcup 1968; Smith and Balda 1979). Nuthatches and chickadees are winter residents in western coniferous forest and often form loose flocks with other seed eaters during the fall cone-opening period and during winter (Stallcup 1968, 1969; Ligon 1973). Foraging has been reported on the squirrel-dropped cones of sugar pine (Tevis 1953), and in the tree on ponderosa pine (Curtis 1948; Stallcup 1968; Ligon 1973; Smith and Balda 1979).

A food habits study of three nuthatch species (table 1) in western Oregon showed the bulk of their diet from May 1969 through February 1970 to be insects (Anderson 1976). Birds were collected from Douglas-fir and ponderosa pine forests but conifer seeds were not listed in their diet, or cone crops mentioned. Because seed-eaters are opportunists adapted to irregular supplies of tree seed it may not be evident in their diet some years. However, the red-breasted nuthatch (Sitta canadensis) was reported taking ponderosa pine seed in Idaho (Curtis 1948), spruce (Picea spp.), fir (Abies spp.), and pine in Arizona (Smith and Balda 1979), limber pine and southwestern white pine in New Mexico (Benkman and others 1984), and is the only nuthatch observed to hammer open pinyon pine seeds with its bill (Smith and Balda 1979). It is also the only nuthatch that is in the group of nine North American boreal tree-seed eating birds showing eruptive migrations (Bock and Lepthien 1976). The white-breasted nuthatch (S. carolinensis), although presented by Smith and Balda (1979) as having the least specialized diet, appeared with the red-breasted taking ponderosa seeds (Curtis 1948) and foraging on whitebark and Jeffrey pine cones in California (Tomback 1977). They also feed from fallen cones of sugar pine (Tevis 1953) and ponderosa pine (Stallcup 1968; Smith and Balda 1979).

The smallest nuthatch, the pygmy (S. pygmaea), occurs west of the Continental Divide up into southern British Columbia. Like the others, it has been observed storing ponderosa pine seed taken from cones on the ground and from the tree in late fall and through winter (Stallcup 1968; Ligon 1973). Smith and Balda (1979) describe its feeding rate on a ponderosa pine cone as one seed extracted per second and the entire cone searched in under one minute.

Nuthatches exhibit intense foraging behavior, like all bark-searching birds who probe for insects, and their strong, narrow, relatively long bills are quite suited to probe the parted scales of conifer cones. But their feeding capability is limited to open cones in the period after squirrels, jays, and crossbills harvest, and in company with chickadees and finches. They also appear to store seeds for relatively short periods (days), cannot carry any quantity beyond one or two seeds, and have an evolutionary orientation for storing in rather limiting locations (bark or tree-trunk crevices) (Smith and Reichman 1984). These characteristics suggest far less predator efficiency than that associated with jays or squirrels. Without more thorough evaluation of seed predation nuthatches probably can't be rated a serious factor in seed loss. The red-breasted nuthatch appears to be more dependent on conifer seed then the pygmy or white-breasted nuthatch because it periodically moves great distances beyond its normal timber habitat, as in 1969-70, when Bock and Lepthien (1976) saw red-breasted nuthatches working on cemetery fenceposts in eastern Colorado prairie far from any tree.

Finches.--Finches (Fringillidae) are agile birds who coordinate their feet and bills, parrots-like, to clamber over conifer cones and search for seed. A finch characteristic is a specialized bill that is internally grooved along each side of the upper mandible. The sharp rim of the bottom jaw fits into this groove to hold and crack seed, a process in which the tongue manipulates and holds the seed in position. Bills vary in groove width, jaw strength, and external shape, thus limiting the size, hardness, and location of seed that can be used by a particular species. The pine siskin (Carduelis spinus) uses its long narrow bill as tweezers to insert between and even pry open cone scales to pull out seed, an adaptation allowing it to exploit many conifer species (table 1; Bent 1968; Newton 1973) but the stubby-billed common redpoll and house finch are probably not as adept or efficient at cone-feeding.

The hooked, crossed tips of crossbill (Loxia spp.) mandibles are uniquely formed to extract seed from hard, closed cones of most conifers, but the shape precludes ground foraging since the tips do not converge enough to grasp small seed. For closed cones the bill tip is inserted behind a scale and the lower mandible moved sideways by powerful muscles to separate the scales and release the seed. Then the specially adapted tongue (longer than other finches with an extra piece of cartilage on the end) scoops the seed out. Closed cones are usually wrenched off the branch and fed on while perched, using one foot as a clamp. According to Newton (1973) crossbills usually take only a few seeds from closed cones then drop the cones. These show frayed and split scales. At seed-dispersal time, crossbills feed while clinging to the cone, similar to other birds.

None of the finches store food, unlike all but the woodpeckers in table 1. This means they do not have a "banking" mechanism to prolong seed predation beyond the dispersal period. With few exceptions the Inland West conifers disperse most of their seed between late August and November. Trees that do extend seed dispersal into winter or longer, and can provide winter food, include western larch (Larix occidentalis), blue spruce (Picea pungens), west coast Douglas-fir (Pseudotsuga m. var. menziesii), western hemlock (Tsuga heterophylla), and the P. p. scopulorum variety of ponderosa pine in Colorado (Schopmeyer 1974). The indehiscent whitebark pine cones can retain seed for months if squirrel or jay predation is not complete. Serotinous lodgepole pine is seldom included as seed prey for birds because cones would either be impenetrable for most birds or an energy-inefficient food source. Lodgepole pine seeds were only 2 percent of the cone weights measured by Smith (1970), compared to 7.4 percent (Douglas-fir), 11.1 percent (ponderosa pine), 14.5 (Engelmann spruce), and 25.9 percent (subalpine fir--Abies lasiocarpa). Animals obviously benefit more by feeding efforts that secure large seed.

Red crossbills were observed near Missoula, Montana, fluttering around ponderosa pine cones and extracting seed from them on 9 May 1966. About the same period, farther west, chipmunks (Eutamias spp.) were seen up in ponderosa pine, clipping cones that retained seed from the 1965 crop (P. F. Stickney and R. F. Schmitz, pers. comm.). Ponderosa pine normally sheds 90-95 percent of its seed between September and the end of October in Idaho and western Montana (Fowells 1965; Shearer and Schmidt 1970). The year 1965 was particularly cold and wet from March through October, with the coldest September in 86 years. The remaining winter was one of the mildest on record. Dispersal of the 1965 seed crop apparently was unusually delayed by these climatic conditions, allowing extended foraging.

Seed can be exposed longer to predispersal predators when a wet fall inhibits cone opening. Normally, seed is released by a drying process where the scale fibrils shrink and contract, to draw the scales apart (Harlow and others 1964). Scale spreading takes place gradually over days and weeks and varies within and among individual trees. Cones also open and close, depending on humidity, causing discontinuous or delayed shedding beyond the normal dispersal period, at least for spruce, pine, and Douglas-fir (Shearer and Schmidt 1970; Allen and Owen 1972; Schopmeyer 1974; Hoff and Coffen 1982).

Irregular seed production and aberrant dispersal patterns are the norm however, and the foraging pattern for finches is most nearly a catch-as-catch-can matter. Such is reflected both in the intensity of seed-foraging and the restless movements of particularly the crossbills and pine siskin. Curtis (1948) singled red crossbills out as the most "voracious" feeders, present in the largest numbers, among nine bird species that descended on a medium-heavy ponderosa cone crop near Idaho City, Idaho, starting about 10 September 1947. Feeding birds persisted until early November in groups up to 40, although numbers peaked in mid-October. A rapid buildup of red crossbills also occurred at Yellow Bay Biological Station in western Montana between Aug. 1-15, 1954 (Kemper 1959). The population showed both physiological (gonadal) and morphological (brood patch, enlarged cloaca) breeding signs. These changes were attributed to excellent cone crops among Douglas-fir, grand fir, and Engelman spruce, and a moderate ponderosa pine crop.

Mammals

The Order Mammalia contributes relatively few vertebrates to the group who take seed in the tree, if compared to birds (table 1). The flying squirrel of the west (Glaucomys sabrinus) is endemic to coniferous forests but is omitted from my listing because I found no firm data that established its conifer seed eating activity, much less using cones still in the tree. Four flying squirrels nearly starved on an ad libitum diet of white spruce (P. glauca) seed, preferring laboratory chow and many other foods instead (Brink and Dean 1966). By contrast, red squirrels preferred spruce cones over the chow, taking 2-3 weeks to adapt to the processed food. Stomach contents of flying squirrels collected each month in California conifer stands showed year-long use of chiefly fungi and lichens but no seed, despite conifer seed being easily available in fall (McKeever 1960). Tests of flying squirrel food preference by Laurance and Reynolds (1984) did find they readily accepted pinyon nuts. Additional study is required because flying squirrels have been popularly accused of damaging conifers by clipping branches and terminals if not cones (Tom Lawrence, pers. comm.).

Red Squirrel.--As an acknowledged seed predator wherever it lives in North America (Murie 1927; Hatt 1929, 1943; Tevis 1953; McKeever 1964; Brink and Dean 1966; Smith 1970; Harvey and others 1980; Benkman and others 1984; Smith and Reichman 1984), the red or pine squirrel (table 1) cuts cones of all conifer species and stores them in winter larders or middens (Murie 1927; Finley 1969; Smith and Reichman 1984). These middens provide necessary energy for over-winter survival. They also supply sustenance needed during the later winter-early spring breeding period when other food is scarce. Each squirrel normally has at least one primary and several secondary middens (C. H. Halvorson, unpublished) which, in abundant crop years, are stocked with as many cones as can be secured prior to seed shedding.

In heavy seed years squirrel caches can supply food well into the second year beyond the crop harvest (C. H. Halvorson, unpublished), thus, the effect of a crop failure is not immediate. With such a food supply concentrated at great effort, it is understandable why squirrels call aggressively if intruders pass through the area of harvest. Red squirrel aggressiveness has long been considered territorial defense. Smith (1968), in southern British Columbia, has described territory size as varying inversely with food abundance but defended all year. Unchanging territorial boundaries were depicted by Rusch and Reeder (1978) in Alberta spruce and pine. Territoriality in a Colorado lodgepole pine forest was not dependent on large central stores because middens were highly variable in size and cone content (Gurnell 1984). Lodgepole pine stands differ from most conifer forests because a seed supply is always available in serotinous cones on trees, as well as in squirrel caches. My studies (C. H. Halvorson, unpublished) suggest that territorialism in the rigid sense of Smith (1968) may not be a constant nor perhaps appropriate concept to describe red squirrel behavior, although it certainly can be a perception. I have found food supplies to be defended and competition existing for areas in which middens were prominent features. However, the degree to which defense took place was more dependent on season, on population density, and on the year of the conifer seed supply than on a sustained and perpetual reactiveness. Their territorial calling (Smith 1978) is never a seasonal or yearly constant. However, red squirrels are solitary year-long, except for an apparent one-day mating period (Smith 1968). Therefore exclusiveness, how and whenever achieved, is distinctive to the species.

Red squirrel tree nests (less commonly underground) are globular and composed of grass, moss, needles, and twigs. The nest is usually one of several in the same or nearby tree. Nests and primary middens are always in proximity, usually 50 ft or less.

Published figures of red squirrel densities from across its geographic range are reviewed and tabulated in Rusch and Reeder (1978). Spring densities varied from about 1 acre (0.4 ha) per adult squirrel in spruce to 19.8 acres (8.1 ha) per squirrel in eastern hardwoods. In my 12-year study (unpublished data) minimum and maximum densities in Douglas-fir/ponderosa pine were 4.5 acres (1.8 ha) to 0.8 acres (0.3 ha) per adult in spring and slightly higher in fall, on the average. This variation illustrates the nature of squirrel populations--they can fluctuate greatly between years. This variation seems universal in tree squirrel populations (Gurnell 1983; Heaney 1984), and is often associated with tree seed abundance (e.g., Sciurus vulgaris in Finland - Rajala and Lampio 1963; T. hudsonicus in Alberta - Kemp and Keith 1970) in theory but not by proven hypotheses.

The red squirrel's characteristic cone clipping on ponderosa pine and Douglas-fir starts almost tentatively in late June and early July after seed fertilization. Douglas-fir and ponderosa pine cones are cut and peeled, usually in the tree or on a favorite feeding log or stump. The time at which red squirrel primary use of cones shifts from feeding to caching coincides with seed maturation, as it does with the Clark's nutcracker (C. H. Halvorson, unpublished; Tomback 1977). Seed maturation is marked by biochemical changes, the more important being a sugar content decrease and a fat increase in the endosperm (Rediske 1961). As mentioned earlier, fat resists spoilage, especially in the cool sites that squirrels select for middens (Shaw 1936; Hatt 1929; Finley 1969). Adult squirrels usually sever and drop individual cones from the branch, but ponderosa pine cones, being tightly appressed to each other and the shoot, are often dropped by cutting the branch just behind the cluster. This causes loss of cone primordia and any first year cones, and could remove three years of fruit growth. If the cluster happens to be on the terminal shoot, the trees's primary elongation point is also lost. Cone clipping rates can be rapid, almost frantic, and squirrels ignore their early morning and late afternoon bimodal daily activity pattern to work through the day. I have seen squirrels cutting Douglas-fir cones at rates of 4 to 8/min, and eating one cone each 3 minutes for 90 minutes. Giant sequoia cones were cut at rates from three/min to 538 in 30 minutes, or 18/min (Harvey and others 1980). Ponderosa pine cones are often cut and stored individually while fir usually are dropped, to be stored later. In one instance it took about 6.5 min per ponderosa pine cone from cutting to burying.

The quality of cones cached by squirrels is sometimes questioned. White spruce and Douglas-fir cones gathered from stores during the entire caching period were found to be ripe and have better viability than seed collected directly from trees in the same periods; there was no significant increase in viability with later dates of cutting, compared to collections

begun at the onset of major caching (Lavender and Engstrom 1956; Wagg 1964). Similar testing apparently has not been done for ponderosa pine or other conifers. Where cones ripen asynchronously between trees a question arises whether squirrels concentrate first on those trees whose mast ripens first. Olson and Silen (1975) found that coastal Douglas-fir seed showed steady weight increases and improved germination even during the final two weeks prior to seedfall.

Considerable data on cutting variability were gathered during a study of squirrels and cone crops on an island in Flathead Lake in western Montana (Halvorson and Engeman 1983). The years 1962 and 1965 had similarly dense fall squirrel populations, averaging >1/acre (>2.5/ha, fig. 1) between August and November. Roughly 65 percent of the cones counted on marked sample limbs were cut each year, although the number of cones on the limbs differed considerably (fig. 1). A heavy seed crop was produced in 1962, measuring about 11 lb/acre (12 kg/ha) of high quality (61 percent sound) seeds of Douglas-fir and ponderosa pine combined. 1965 had a very light crop (0.30 lb/acre, 0.34 kg/ha), consisting almost entirely of low quality (22 percent sound) ponderosa pine seed. In 1962, the Douglas-fir cutting rate was 8-10 days earlier than for pine, a typical pattern because ponderosa pine cones opened later than fir. By September 10, 1962, squirrels had gathered 179 pine and 636 fir samples cones, or over three-quarters of the sample ultimately removed that year. In contrast, in 1965, only 78 pine cones were cut by September 20 and only 90 total removed, at a desultory rate (fig. 1), by a larger population than present in 1962. Weather in 1962 was a "normal" warm but somewhat dry fall, and 1960 and 1961 had been poor crop years. 1965 had record September cold temperatures and a wetter than average entire year, causing seed to be held in cones (see earlier). In 1965, middens (caches) were still full from a 1964 seedfall of 28 lb/acre (31 kg/ha), the largest in 12

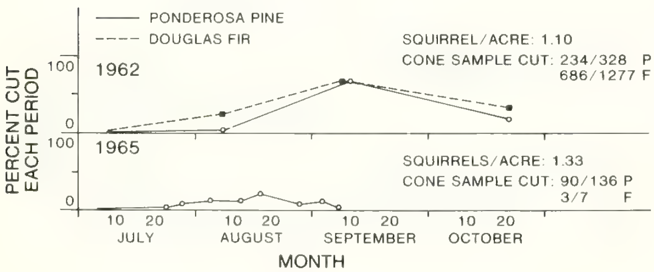

Figure 1.--Variability in cone-clipping rates on tagged-limb samples of ponderosa pine (P) and Douglas-fir (F) cones in a year of heavy (11 lb/acre; 12 kg/ha) cone crops and warm, dry, fall weather (1962), and poor (0.3 lb/acre; 0.34 kg/ha) cone crops and very wet, cool fall weather (1965). Similarly high squirrel densities occurred both years. Cedar Island, Montana (C. H. Halvorson, unpublished).

years. That seed was 60 to 70 percent sound. This example depicts the influence of weather, seed quality, and the availabilty and influenc of previously stored food. To 1965 could be added the greatest abundance of fungi found on the island to that time--an effect from the "unusual" weather that year. Squirrels are known for their catholic food habits (Hatt 1929), especially utilizing the seasonal abundance of fungi and hanging it in trees to dry (Hatt 1929; McKeever 1964; Fogel and Trapp 1978).

Other Squirrels.--Chipmunks and golden-mantled ground squirrels are terrestrial rodents who forage extensively on the ground for seed, fungi, fruit, herbaceous material, and insects (Tevis 1952, 1953; Broadbrooks 1958). Both genera have internal cheek pouches that are effectively used to transport food. Over-wintering strategies differ in that the ground squirrel converts its fall feeding into fat layers metabolized during true hibernation. Chipmunks do not accumulate fat or gain weight before winter but go into torpo that may be interrupted by mild periods during winter. Their strategy of lining their underground nests with seeds allows them ready and safe access to nutritious food during winter awakenings. Broadbrooks (1958) described finding 1080 ponderosa pine seeds in one nest and 5360 Douglas-fir plus about 10,000 herbaceous seeds in another. One cache contained 170 g of seed, about 50 g being pine.

All studies of seed eating in these two genera have dealt with ground foraging for seed and those impacts on tree regeneration (Pank 1974). Seed predation in the tree canopy has been observational and anecdotal, thus we have no measure of its importance, and only sparse data that such foraging occurs. *Spermophilus lateralis* and *Eutamius* spp. have been seen foraging up in conifers. The chipmunks are more agile and seed constitutes a larger part of their diet than it does for the ground squirrel (Ingles 1965). *E. amoenus* has been seen feeding at heights to 100 ft (30 m) in ponderosa pine and Douglas-fir, pulling seed out as cones opened. Broadbrooks (1958) described two chipmunks feeding side by side from the same cone 50 ft (15 m) up in a tree. Whitebark and Jeffrey pine seed were gnawed from cones by golden-mantled ground squirrels and chipmunks in trees amidst seed-gathering by Clark's nutcrackers (Tomback 1977). Benkman and others (1984) in Arizona reported similarly for the two sciurids feeding on limber pine. These reports all describe fall feeding. Dick Schmitz's observation on ponderosa pine seed retained into at least early May and being used by chipmunks was mentioned earlier. None of the accounts I found mention any in-tree behavior other than pulling seeds from opening cones or gnawing cones. Some seed is probably pouched and carried to storage but cone-clipping and caching, a much more efficient form of foraging behavior (Janzen 1971; Smith and Balda 1979; Smith and Reichman

1984) is not discussed. The habit of seeking and pouching individual seed for storage is an evolved feeding characteristic, therefore the most efficient practice for terrestrial sciurids. Cone storing or clipping has not been the adaptive path taken by the chipmunk and ground squirrel, therefore is probably energy-inefficient for them and they would seem to impose minor impact on predispersed seed compared to arboreal squirrels.

Bears.--What is written on bear use of conifer seed in the Inland West comes mainly from Yellowstone National Park (Mealey 1980; Murie 1981; Hutchins and Lanner 1982; Kendall 1983) and northern Montana (Tisch 1961). Both the grizzly and black bear (table 1) eat whitebark pine seeds and berries as the main fall food, when available. Spring use of pine seeds is also a matter of availability if the previous fall had a heavy cone crop (Kendall 1983). Limber pine seeds are mentioned as grizzly food only by Craighead and Craighead (1972) and C. Jonkel (pers. comm.). The seeds are obtained by robbing red squirrel cone caches or rodent seed stores (Mealey 1980; Hutchins and Lanner 1982; Kendall 1983) but relatively little by climbing trees (black bear only--Tisch 1961). Therefore, bears would be secondary predators on cones and only on two noncommercial pines. Murie (1981) in Alaska suggested that spruce cones were not palatable, otherwise they would be expected to appear in grizzly droppings during heavy crop years when squirrels pile cones above and underground. Both bear species are able to extract seed without ingesting cones scales, therefore scales don't appear in scat. Bears feed by breaking cones up in their mouth or underfoot, then licking the seed up and expelling scales from sides of the mouth (Kendall (1983). In summary, bear feeding concentrates on noncommercial pines, depends mostly on squirrels storing cones, and is tied to periodicity of good cone crops. At least the two large-seeded pines are recognized as very important fall foods in the northern Rocky Mountains, and are sought after in spring prior to herbaceous vegetation growth (Kendall 1983).

VERTEBRATE IMPACT ON PREDISPERSED SEED

The known impact that vertebrates have on reducing potential seed crops depends on factors of economics, species characteristics that contribute to feeding efficiency, amount of study, and the response or dependencies of animals to crops. To portray relative importance, I have distilled from the foregoing accounts those qualifications that potentially affect or relate to species relative impact (table 3).

Judging Importance

The categories of table 3 list: 1) whether the species has been studied with the purpose and detail needed to quantify their effect on seedfall, has been only described, or has not been observed in measurable terms; 2) the economic status of food trees; 3) specialized and efficient feeding behaviors (beyond simply extracting seed from cones in trees or moving normal distances to exploit a food source, once located); 4) unique morphological adaptations that increase foraging effectiveness (beyond standard family attributes like gnawing incisors or grooved bills). The fifth category concerns responses to seed crops rather than impacts. It infers the importance of cones to animals by listing some responses that occur from cone scarcity or abundance, but also suggests the extent of evolutionary adaptiveness to cone crops. Winter residency is not shown in table 3, but would qualify a bird as a potentially more effective predator than transients. The white-headed woodpecker is the only bird listed whose eastern winter range stops at western Montana.

Species importance can be interpreted from table 3 by tabulating the number of categories having a positive (yes) statement and how many "Special" factors are assigned. Animals feeding on noncommercial whitebark, limber, or even the commercial seed of pinyon pine (Fowells 1965) would be of little concern to the timber industry regardless of how well studied the animals were. Thus, bear use of whitebark pine cones would be of major interest only to agencies managing these omnivores, especially since bears are secondary predators on cone crops. Siskins and redpolls would be of less relative importance even though they double their breeding period in response to unusually abundant spruce seed (Newton 1973), but they only feed exploitatively without caching when a crop appears. However, both species show irruptive migration and their impacts have not been measured. Benkman (pers. comm.) classed the pine siskin as a major but temporary predator on tamarack (Larix larcina), its competitor being the white-winged crossbill. Nuthatches and chickadees are birds that simply pull seed out and cache them individually in bark crevices, as they do other prey. The pygmy nuthatch is reported to extract one ponderosa pine seed/sec. and work one cone/minute (Smith and Balda 1979). Their impact is far less than the crossbills' who can attack closed cones effectively with their laterally abducting mandibles, irrupt, and breed as a result of stimulus effect from abundant cones (Kemper 1959; Newton 1973; Bock and Lepthien 1976). Although finches exploit but do not store food, the crossbills especially are extremely effective predators because they range widely in large flocks and can open cones. In high-value sites, such as seed orchards and nurseries, they have potential to consume large amounts of seed on a local basis (Curtis 1948). Their feeding potential is unmeasured.

The Important Vertebrates

Any bird or mammal that feeds on open and closed cones of commercial tree species, has

Table 3.--Status[1] and ordering of factors that relate predispersal seed users to conifer cone crops

Species	Impact & Feeding Quantified	Commercial conifers	Special feeding behaviors	Special morphology	Special Response to cone crops
Hairy Woodpecker	No	Yes	Closed and open cones	Strong bill, feet	Unknown
W.-headed Woodpecker	Yes-limited	Yes	Slash green cones	Strong bill, feet	Unknown
Gray Jay	No	Unverified	Not conifer seed	Salivary glands	[2]
Steller's Jay	No	Yes	No	No	Unknown
Pinon Jay	Yes	Yes-limited	Disperse caches	Esophagus expands	Breeding (SW only)[2]
Clark's Nutcracker	Yes	Yes	Disperse caches	Sublingual pouch	Breeding, weight[2]
Blk.-billed Magpie	No	Unverified	No	Buccal cavity	Unknown
Blk.-cap. Chickadee	No	Yes	Cache seed	No	Unknown
Mtn. Chickadee	Descriptive	Yes	Cache seed	No	Unknown
Boreal Chickadee	No	Yes	Cache seed	No	Unknown
Red-brst. Nuthatch	No	Yes	Cache seed	Strong feet, bill	[2]
W.-brst. Nuthatch	No	Yes	Cache seed	Strong feet, bill	Unknown
Pygmy Nuthatch	Descriptive	Yes	Cache seed	Strong feet, bill	Unknown
House Finch	No	Yes	No	No	
Red, W. Crossbills	Descriptive	Yes	Closed and open cones	Prying bill	Breeding[2]
Common Red Poll	No	Yes	No	No	Breeding[2]
Pine Siskin	Descriptive	Yes	No	No	Breeding[2]
Red Squirrel	Yes	Yes	Cache cones	Wrist joint	Breeding, longevity
Chipmunk	Descriptive	Yes	Cache seed	Cheek pouch	Unknown
G.M. Grd. Squirrel	No	Yes	No	Cheek pouch	Unknown
Grizzly & Black Bear	No	No	Rob squirrel caches	No	Concentrate feeding

[1] For European corvids (jays and crows) see Turcek and Kelso 1968.
[2] Periodic irruptive movement and (generally) southward invasions (Bock and Lepthien 1976).

particularly effective feeding behaviors and morphology, and shows a distinctive response that suggests strong dependency on cone crops would qualify as the potentially most effective predator on predispersed seed. These criteria quickly narrow the list to four vertebrates: the white-headed woodpecker, pinyon jay, Clark's nutcracker, and red squirrel (table 3). The white-headed woodpecker's propensity and efficiency in slashing open green cones (Tevis 1953) suggest they be especially identified in seed orchard management, the same as crossbills. White-headed woodpeckers have been studied little and their importance to cone crop impact is undetermined.

For the most part bird foraging on conifer cones is scattered and sporadic throughout forest stands during seed ripening, and is not conspicuous like that seen in cultivated crops (ducks and grain, blackbirds on rice and sunflower seeds) where loss is assessed in bushels or tons. Even concerted effort by researchers often achieves only approximations of agricultural seed loss (J. Besser, pers. comm.). However, some quantitative estimates of seed removal by Clark's nutcrackers and pinyon jays have been possible because the seed capacities of the nutcracker's sublingual pouch and the jay's distensible esophagus are known. Swallowing a seed completely or pouching it is distinguishable by the slight backward head toss which accompanies pouching (Tomback 1977). By counting the number of daily trips an individual nutcracker made with filled pouches, Tomback (1982) was able to estimate seed take. A singl bird might store about 32,000 whitebark pine seeds in a good crop year, or 3-5 times its energy requirements, thus leaving seed for germination, rodent food, and other fates. Twenty-five birds foraging their average 4.5 hr/day for the approximate 42 day storage seas were estimated as caching about 800,000 seeds (18,000 cones) in a 125 acre (50 ha) area. Thi was about 200,000 seed caches. From 75-100 percent of the whitebark pine cones were destroyed or partly eaten by nutcrackers and chipmunks in 1979 on Tomback's (1981) tree transects. Similar high losses of limber pine cones occurred in Utah where 90 percent (1322) were removed in 1979 and 70-90 percent even in the preceding bumper crop year (Lanner and Vander Wall 1980). The major result of unrecovered seed caches that germinate is the frequently seen multiple stemmed occurrence of whitebark pine. Tomback (1977) found 1 to 4 (mean 1.7 ± 1.0) seedlings per cluster in a Sierr Nevada burn where nutcrackers were storing seed. This corresponded to the average of 3.2 ± 2.9 (minimum 1 to maximum 15) seeds per cache recorded. Multiple-stems are also frequent on a Utah burn where nutcrackers are similarly reestablishing limber pine (Lanner an Vander Wall 1980).

Ligon (1978) observed flocks of 200 to 300 pinyon jays and calculated conservatively that they stored 30,000 seeds/day and perhaps 4.5

million seeds in the September-January storage period. He noted they frequently select very open areas (e.g., areas cleared of pinyon-juniper) to store seed next to shaded, moisture-favorable sites such as bushes or downed trees and away from competition with the parent tree.

Cone ripening phenology is a factor in seed loss --the "satiation" principle mentioned earlier. Benkman and others (1984) speculated that nutcrackers could take 6.6 percent of a limber pine seed crop because the cones appeared to ripen simultaneously on individual trees but asynchronously among trees. But if cones on all trees ripened together, which they interpreted for southwestern white pine, foraging would not encompass the entire crop before seed shed and only 3.7 percent would be harvested. Because seed-eating birds tend to concentrate their harvesting in flocks, seed loss would depend on seed-ripening patterns of conifers. Total loss contribution from birds is also related to the presence or absence of tree squirrels. Red squirrels took about 80 percent of an Arizona limber pine crop and nutcrackers harvested about 1.6 percent, whereas the birds gathered 12-22 percent when squirrels were absent (Benkman and others 1984). In assessing the impact of vertebrates on predispersed seed, the cone ripening pattern of conifer species should be identified and the contribution of seed-cache germination to re-establishing tree stands should be considered.

The Red Squirrel As A Cone Predator

The red squirrel's superior efficiency as a predator stems from its ability to rapidly collect large quantities of seed by cutting cones. The Clark's nutcracker and pinyon jay also gather seed in groups but their seed extraction and storage does not appear as efficient. I timed a red squirrel cutting ponderosa pine cones and carrying them from the tree to a cache and back at 6.5 min/ cone (6 cones). This equaled one seed stored each 6.5 sec, using a figure of 60 sound seed/ cone (Schmidt and Shearer 1971). It took nutcrackers an average of 24 (11-66) min to harvest one pouch load (77 seeds) of whitebark pine and return from caching them; an average of 19 sec/seed (Tomback 1982). However, whitebark pine seed is 4.6 times heavier than ponderosa seed (Schopmeyer 1974), reducing the weight equivalent carried to about 4 sec. But nutcrackers took 31 sec to extract seed from closed cones (7 sec for open ones) where the cutting rate for squirrels is unaffected by cone stage and squirrels harvest continually through the day in the presence of cone abundance. Nutcracker harvesting conservatively takes 4.5 hr/day (Tomback 1982). Guintoli and Mewaldt (1978) only recorded 25 ponderosa seeds per pouch (n=20) in Montana, suggesting far less efficiency than Tomback measured. A radio-collared squirrel (C. H. Halvorson, unpublished) was tracked for 90 minutes during which time it cut, peeled, and consumed the seed of 30 mature but closed Douglas-fir cones, i.e. 1 seed/4 sec or 3 min/cone, including some movement to reach cones in the trees. In other observations squirrels cutting an average of 6 (4-8) fir cones/min were removing 270 seed/min or 1 seed/1.3 sec. (about 45 seeds/cone using Finley 1969). The fact that squirrels guard their caches and caches are available only to bears increases greatly the squirrel efficiency.

The proportion of a cone crop harvested by red squirrels varies considerably and the effect on seedfall is not stated simply. Many harvest figures can be quoted: sugar pine 54 percent (Tevis 1953); limber and southwestern white pine 75-83 percent (Benkman and others 1984); ponderosa pine 19-82 percent (Schmidt and Shearer 1971); Douglas-fir 17-100 percent (C. H. Halvorson unpublished). Tevis (1953) noted that the harvest on individual trees also varied from 11-100 percent. In a study of ponderosa pine cone loss factors in Montana (Schmidt and Shearer 1971), the amount of cutting by squirrels could not be related directly to crop size but may have been affected by both the abundance of the companion conifer, Douglas-fir, and the weather. The pine cone harvest was inverse to the size of the fir crop. With a 1954 heavy fir crop (229,000 sound seeds/acre) only 19 percent (24 of 125 sample cones) of the pine cones were cut. This was a cool, moist fall. When the fir crop failed in 1956, during a warm, dry fall, 82 percent (40 of 49 sample cones) of a visually estimated light pine crop was removed. Intermediate to these rates was a 54 percent removal (69 of 128 samples cones) of a light (7,100 seeds/acre) pine and fir crop during average fall weather.

Many combinations of cone abundance, harvest, and squirrel population occurred between 1962 and 1972 (table 4) on the Flathead Lake study island (C. H. Halvorson, unpublished annual rept.). A medium-density (0.96 squirrels/acre) population took about half of a fair pine and fir crop (about 4 lb/acre total) in 1967 but the same density cut only about 18 percent of sample cones in the very heavy crop year of 1971 (21.7 lb total seed/acre). The seed-fall amounts (table 4) would all be adequate for regeneration, except for the 6000 fir seed/acre, but varying amounts are also taken by ground-dwelling rodents and would further reduce potential germinants. Seed abundance and the proportion of cones taken by squirrels determine how many seed reach the ground and that is variable but important information to a forest manager.

Previous studies have only reported cone crop abundance and loss without determining squirrel population densities. But even with densities accurately known it has not been possible to establish a simple linear relationship between squirrel numbers and cone loss (C. H. Halvorson unpublished). The correlations between cone crops of either the same or previous year and August and November squirrel densities have been of low order (r=0.581 to 0.381), suggesting that

factors other than crop levels determine squirrel densities and the proportion of a cone crop taken--factors such as other food availability, cone quality, predation, competition, breeding-age ratios, and weather (C. H. Halvorson unpublished). The study by Sanders (1983) on foraging by the Douglas squirrel T. douglasi in California similarly reported a lack of correlation between crop size and the proportion of white fir and Jeffrey pine cones taken. She concluded that squirrels foraged according to food encounter or energy intake rates rather than to an expectation of the cones quantity to be removed. Sanders also found evidence that squirrels with more cones on their home ranges took a significantly lower proportion of available cones than squirrels on cone-poor areas.

Seed quality is an important factor that enters into our perception and examination of cone abundance, the cone-cut, and squirrel population relationship. Douglas-fir apparently can develop full size cones without pollination or fertilization (Allen and Owens 1972). Ponderosa pine and other conifer cones also can develop normally with a low level of fertilized seed (Geo. Howe pers. comm.). Viewed from the ground in early summer, a good cone crop can be forthcoming but the promise of a crop is a familiar one to foresters. In this northern region, the year 1978 looked good for lodgepole and ponderosa pine, western larch, spruce, and fir but, except for yellow pine, the seed quality was poor in the presence of a very wet spring (John McBride pers. comm), suggesting possible pollination disruption because most species, except pine, have a one-year development cycle. Cone insects, especially Hemiptera (e.g., Leptoglossus occidentalis) are especially adept at inconspicuously damaging maturing cones that otherwise appear normal. Red squirrels, as with other seed predators, readily detect and reject poor quality food, often without having to sample it.

The total effect of squirrel clipping, from ovulate bud formation to seed germination, has been measured for ponderosa pine in Montana by Schmidt and Shearer (1971). In the first year of cone development, squirrels removed only 2 percent, the female strobili being associated with mature cone-bearing shoots ends that squirrels are prone to clip. About 44 percent of mature cones were lost the second year, the figure varying yearly as outlined earlier. A 14 percent loss of the potential cone crop was the combined effect of squirrel impact during the two-year cycle.

Squirrel Clipping of Buds and Shoots.--Red squirrels also indirectly affect cone production by their feeding on buds, clipping branch ends, and girdling in the tree crown. There are many such references for all tree species squirrels associate with (Hosley 1928; Hart 1936; Shantz-Hansen 1945; Rowe 1952; Cook 1954; Duncan 1954; Adams 1955; Lutz 1958; Walters and Soos 1961; Pulliainen and Salonen 1965).

In my experience, reproductive buds of Douglas-fir were often incorporated as food, but only when squirrels were hard-pressed for cones did they concentrate over-winter feeding on buds. In the spring of 1967 on Cedar Island, I found Douglas-fir twigs with primarily pistillate but also staminate buds eaten. Twig density over most of the island was 20-25 per 3 ft^2 (0.84 m^2) sample (C. H. Halvorson unpublished). Foresters elsewhere in the northern Rockies reported peeled basal ends of ponderosa pine shoots (see Adams 1955), needles fed on, and pine shoots blanketing the ground where squirrels lived. Specimens I examined showed typical squirrel tooth patterns. Cone crops in the region for two years prior to 1967 had been poor, and I attribute the feeding directly to lack of cones.

Terminal and lateral shoot clipping causes concern for tree form and lumber quality but

Table 4.--Cone crop harvest rate and residual seedfall in different crop years and levels of fall (Aug.-Nov.) squirrel densities. Cedar Island, Montana (C. H. Halvorson, unpublished)

Year	Squirrels per acre (ha)	Potential crop[1] P. pine	Potential crop[1] D.-fir	Cone harvest (%) P. pine	Cone harvest (%) D.-fir	Residual seed[2] P. pine	Residual seed[2] D.-fir
1962	1.1 (2.7)	5.4	5.4	71	54	15	106
1964	1.8 (4.5)	7.8	20.2	83	80	19	172
1967	0.9 (2.2)	3.6	0.3	55	53	19	6
1971	0.9 (2.2)	12.8	8.9	17	20	127	300

[1]Pounds per acre (kg/ha = 16/acre x 2.2046 ÷ 2.47).
[2]Thousands per acre (seed per ha = 1000/s ÷ 2.47).

oastal Douglas-fir saplings showed no height oss after three growing seasons where terminals ad been clipped off by squirrels (Fisch and imock 1978). The injury was considered minimal nd temporary by the authors, similar to Rowe's 1952) opinion for white spruce. Lutz (1958) bserved that the club-top or tufted appearance f black spruce could be ascribed to squirrels utting twigs in the apical aggregate of cones hat characterizes the species. The bare bole ection below the top functioned as a fire-break nd prevented destruction of the cone crop. The ffect of terminal clipping in conifers can be ultiple- or fork-tops, but Hoff and Coffen 1982) saw little height difference between erminally pruned compared to unpruned ingle-stemmed western white pine in a seed-tree lantation. Because multiple-topped trees roduced more cones and pollen, the authors ecommended that leaders and terminal buds of lantation trees be pruned to maintain 1-3 stems rom the 10 ft (ca. 3 m) height upwards.

lthough I believe from field observation that he stag-horn branching appearance of mature and overmature" ponderosa pine is a direct result f red squirrel feeding activity, whether for ones or survival in coneless years, it remains o be proven that shoot pruning (with ccompanying apical bud removal) increases ollen and cone production in wild trees as it oes for cultivated western white pine (Hoff and offen 1982). Pruning buds in higher plants timulates branching and there would seem little rgument that squirrels are stimulating pine ranching. If more cones are produced, the quirrel benefits.

n summary, red squirrel total impact can be 14 ercent of a potential ponderosa pine crop Schmidt and Shearer 1971) but is unknown for ther conifer species. Cone harvest is highly ariable and crop size is not directly related o harvest rate. However, expressing the impact f squirrel cutting simply as the proportion of ones cut has little meaning to forest anagement without knowing crop quality and size f both the potential and residual seedfall. ven heavy loss of a bumper cone crop is likely o produce adequate seedfall for germination, ut a light harvest of a poor or fair crop robably will give an inadequate seed supply. nmeasured but real value can be assigned to quirrel cone harvest because some of the 14 ercent total impact on potential crop, or 66 ercent on immediate cone crop, is recoverable rom caches for nursery planting (Finley 1969). alue can also be postulated for bud and shoot njury by squirrels, at least in terms of nhancing fruit production and food production tructure of some tree species, but this too is nmeasured. While birds are primarily xploitive on cone crops, at least the Clark's utcracker and pinyon jay have been shown to enefit the distribution of noncommercial, arge-seeded pines in the absence of any active anagement programs by agencies for those pecies.

ANIMAL RESPONSES TO IRREGULAR CONE CROPS

Animal response to changes in prey density has been described as either numerical (Solomon 1949), or functional (Morris and others 1958). If the prey (cones) density changes and predators show increased numbers the response is termed numerical. It could include breeding effect but also the irruption phenomenon described by Bock and Lepthien (1976). Red squirrels also appear to respond numerically with increased breeding effort. A functional response occurs where access to increased prey (cones, seeds) tends to concentrate or shift foraging activities onto that prey (Morris and others 1958). The sense of "functional" has been typified mostly in forest insect outbreaks where birds actually shift from their usual foods. All seed predators show a functional shift by including more seed in their diet when it is available; some birds going back to buds and insects when the seed supply fades, or emphasizing an alternative conifer species if available. A physical response was seen in Clark's nutcrackers who weighed significantly less the winter after cone crops failed to appear in western Montana (Guintoli and Mewaldt 1978). Underweight nutcrackers in Utah in 1977 (Vander Wall and others 1981), were thought to be recent immigrants because resident birds were feeding normally on an abundant pine crop. In 1977, all cone crops in the U.S. Forest Service Northern Region were reported poor; also very spotty in 1976 (U.S.F.S. Reg. 1 Nursery Reports and R. Shearer, pers. comm.).

The stimulus effect of food (Kemper 1959) and the exploitive flocking to cone crops as they ripen is typical of crossbills (Newton 1973; Bock and Lepthien 1976); this was similarly recognized in the pinyon jay by Ligon (1978). Crossbills are also known to breed in any month, in response to cone crop abundance, but chiefly in late winter and then again late summer. Pinyon jay's second breeding in June and July (Ligon 1978) is also ascribed to food stimulus, in this case when abundant green pinyon cones are maturing. Even pine siskins and redpolls will double their breeding period in the presence of unusually abundant spruce seed crops (Newton 1973).

In summary, Nearctic redpolls, pine siskins, and crossbills all move seasonally in response to seed-ripening or in response to availability, wherever cones still hold seed. When fall conifer crops are found, the birds settle on those until the seeds are mostly eaten up or shed, then travel to the next supply. Crossbills will go into a breeding condition anytime the new supply is plentiful (e.g., Kemper 1959). The periodic mass movements ("irruptions") are also food-related but only the crossbills depend on conifer seed in cones throughout the year. When mass migrations occur, and six of the irruptive species are finches (Bock and Lepthien 1976), a combination of food shortage and large populations is believed responsible (Newton 1973). However,

Tomback (1977) suggests that a bird such as Clark's nutcracker that is intricately tied to conifer seed may only need total failure of all its conifer seed resources to irrupt, in spite of population density. The crossbill is similar enough to the nutcracker in tactical respects that it could be convergently responding the same way, or else has evolved to move and compensate for local crop failures.

Squirrel life history also contains response to cone crop abundance that may serve to drive the mechanism postulated earlier in this section, but the way this happens is still being examined (C. H. Halvorson, unpublished data). Gurnell (1983) summarized responses from the European and American literature on all tree squirrels species: "...seed availability can affect the length of the breeding season, the number of adults which produce two litters, the number of adults and yearlings which breed, and the mean litter size at birth and weaning." Not mentioned is evidence that adult squirrels, if born in high seed crop years (5 lb/acre; 5.6 kg/ha), show a median longevity of 17 months compared to 22 months for births in a poor crop year (C. H. Halvorson and Engeman 1983). I also found the breeding incidence among yearling red squirrels on Cedar Island to be 88 percent in high crop years and 51 percent in low years, a not quite significant difference and low correlation ($p=0.052$, $r=0.628$) with crop years, but crop years may not be the largest source of variation in the repeated measure ANOVA used (Halvorson unpublished; also Gurnell 1983 citation). However, an analysis of litter size difference between high and low seed abundance years showed that production of young was predictably and significantly greater if seed was plentiful ($p<0.00003$, $r=0.95$ for number of young per female). Finally, I found that in the 12-yr study some females had second litters only in the three heaviest seed crop years, 1962, 1964, and 1971 (C. H. Halvorson unpublished data), thus providing further direct evidence that squirrel populations respond to conifer seed abundance. This association has often been inferred but until now has not been previously established on a basis of both measured seed crops and accurately counted squirrel populations--a need expressed by Gurnell (1983).

SUMMARY

I have presented the names and nature of seed-eating vertebrates common to the North American West but particularly to the Inland Mountain West where most are resident species. At least 21 of the birds and mammals listed (table 1) make important use of conifer seed before it is shed from the cone. A few other bird species do so to lesser extent. The most effective predators are those who can feed habitually on closed and green cones. These include one mammal--the red squirrel; one woodpecker--the white-headed; two corvids--the pinyon jay and Clark's nutcracker; and two finches--the red- and white-winged crossbills. Except for the white-headed woodpecker whose habits are not well known, the other five have unique behaviors, morphology, and strategies that enable them to effectively exploit cone crops whenever they occur, especially in abundance. The crossbills do not store food, hence must search continuously for cones, but once found, the birds quickly transform the food energy into a reproductive thrust. The squirrel and corvids intensively gather and store food when it becomes available, using it in maintenance and later reproduction, thereby extending their predation period on seed. Corvids somewhat control competition for seeds by burying them. The squirrel eliminates most of its competitors by burying the entire closed cone and making the seed unavailable to all except other squirrels, insects, and bear. The grizzly and black bear apparently use squirrel caches when they contain whitebark and limber pine cones. The remaining predators on predispersed seed must compete for seed that is more accessible in opening cones, and these animals basically exploit an immediate food source or store portions for brief periods of days or weeks.

Those predispersal seed predators most highly adapted and effective on cone crops also return some value by being effective seed dispersers--the case of the nutcracker and pinyon jay--or, if a squirrel, by serving as a source of high quality seed for nurseries (but only if the seed didn't originate from costly seed-tree orchards). Whether benefits to trees accrue from squirrel feeding is speculative, but answerable by further study. The impact of most birds on predispersal seed is not fully assessed from the present primarily descriptive accounts, especially for the commercial conifers growing in this Inland Mountain West.

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SQUIRREL BEHAVIOR INFLUENCES QUALITY OF CONES AND SEEDS

COLLECTED FROM SQUIRREL CACHES--FIELD OBSERVATIONS

Jeanne L. Pedro White and Monte D. White

ABSTRACT: Field observations were made in north-central Idaho during the 1980 through 1984 seed procurement seasons. Squirrel behavior affects the quality, location, species, maturity, and viability of seeds collected. This paper discusses some aspects of collecting seed cones for reforestation from squirrel caches. With proper care in collecting and handling cones, good quality seed can be obtained.

INTRODUCTION

The authors have observed the behavior of pine squirrels during cutting and caching of coniferous seed cones since 1980. Observations were made on the Pierce Ranger District of the Clearwater National Forest and surrounding private forest lands. This paper discusses conventional opinions about squirrel cache collection of seed cones for reforestation. Cache location, cone handling, and relative collection costs are also discussed.

CONVENTIONAL OPINION

Opinions differ on the acceptability of seed collected from squirrel caches. The most prevalent of these and our responses to them are:

Seed Maturity

Squirrels tend to harvest cones before they are mature. Response: Seeds collected from squirrel caches on the Pierce Ranger District had viability ranging from "acceptable" to "excellent", as shown in table 1. These data were obtained from germination test records of the Coeur d'Alene Nursery located in Coeur d'Alene, ID.

Seed Sources

Seed sources are uncertain. Response: Individual source trees cannot be determined with certainty when collecting cones from squirrel caches. However, while checking cone crops of potential collection sites, the authors observed that the majority of cones are to be found in the dominant and codominant trees in even-aged stands. When collecting cones, most squirrel activity was found in those trees. This is probably due to advanced maturity and relative abundance of cones found in the upper canopy. One can be relatively certain that most of the cones found in caches located within the stand were borne by those trees, although some could have been imported from adjacent stands. To ensure genetic diversity, we collected from at least seven separate cache sites within stands. Collection site desirability can thus be based on phenotypic characteristics of the larger stand components.

Squirrels Winter Food Supply

Collection from caches deprives squirrels of their winter food supply. Reponse: Squirrels collect far more cones than they can eat. If available, they will cache seeds from a variety of plants, then fail to find all of the caches. Individuals dying before winter obviously do not return to consume their caches. The authors have found old caches which have evidently remained untouched for years.

Only a portion of the squirrel caches will be found by human collectors. An example of this is that on one occasion cone pickers assigned to collect cones from the tops of felled trees didn't collect all the cones before leaving for the evening. Returning the following day, they found all the cones missing from the trees with no nearby caches to account for them.

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Table 1.--Viability of seeds collected from squirrel caches on the Pierce Ranger District, Clearwater National Forest, ID, 1980-1983

No. of Seedlots		Species	Average Viability	Range of Viability	Seedlots Below Minimum Acceptable Viability[1]
1980:	14	DF	94%	79 - 97%	0
	4	ES	91%	77 - 97%	0
	7	GF	77%	56 - 88%	0
1981:	6	LP	77%	42 - 90%	1
1982:	5	DF	95%	92 - 98%	0
1983:	1	LP	88%	-	0

[1]Acceptable minimums are: Douglas Fir (DF) = 70%; Engelman Spruce (ES) = 60%; Grand Fir (GF) = 50%; Lodgepole Pine (LP) = 70%

FINDING THE CACHES

The art of locating squirrel caches is acquired primarily through experience. Favorite cache sites include: small ground depressions (including animal tracks); cavities in and around logs, stumps, roots, and rocks; moist seeps; along the banks of small creeks; in and around structures such as fences, outbuildings, and foundations. Squirrels may enlarge the storage locations. Cones may be concealed beneath wet moss, cone scales, needles, or other debris and there may be layers of this type material between pockets of cones within the storage locations. Cache volume will range from a few cones to more than a bushel. One will not always be able to find specific types of caches or species of cones in a given area. Squirrels seem quite opportunistic in caching behavior, taking advantage of whatever storage areas are available.

Squirrels will sometimes carry cones amazing distances to be cached. On one occasion, a cone cache was found along a stream bank and the nearest seed source was 10 to 12 chains (200-240 meters) away. Many times squirrels can also be seen carrying cones across roads and skid trails. In most cases, though, cones are cached near or below the source trees.

OTHER CONSIDERATIONS

1) During years of abundance, squirrels seem to prefer true firs and Douglas-fir over pines in mixed stands. White pine cones seem to be less desirable when other species are available in collectible quantities.

2) Cone collection from squirrel caches does no result in damage to the source trees. Human collection results in tree damage. Damage range from incidental bark gouging and branch breakage when using "cherry pickers" or climbing spurs, t seed tree destruction, when trees are felled pri to cone picking.

3) Cone collection costs will usually be lower cones are obtained from caches than by more labo and equipment-intensive means.

PROPER CONE HANDLING IS IMPORTANT

Cached cones are often wet, dirty, and/or insect damaged. With proper on-site sorting, the colle can dispose of most undesirable cones. If cones wet, storage of fewer cones per bag will speed drying time and prevent molding. If sound colle procedures are followed, good quality cones will usually be received at the collection station.

CONCLUSIONS

Squirrel caches are now a major source of refore tion seed on the Pierce Ranger District. Viabil tests from the Coeur d'Alene Nursery on squirrel cached seed show that mature, viable seed can be obtained in this area using the cache collectior method. Caches can be found in diverse locatior although, at times, they may be difficult to loc Cache location experience combined with proper c handling during and after collection will usuall result in high-quality reforestation seed in sto

INSECTS AND CONIFER SEED PRODUCTION IN THE INLAND MOUNTAIN WEST: A REVIEW

Gordon E. Miller

ABSTRACT: Hundreds of insects are associates of cones and seeds in the Inland Mountain West, but only a few cause economic damage. Damage by insects is one of the major impediments to seed production in Douglas-fir, spruces, ponderosa pine, western white pine, and western larch, based on the few published damage surveys from the region. Each tree species has its own complex of associated insects. Salient features of the bionomics to development of pest management systems are discussed. Major short-comings in the management of insects affecting seed production are the lack of methods for monitoring pest populations and the limited options in pest control.

INTRODUCTION

Cone and seed insects are major impediments to seed production by many conifers. Hundreds of insect species are known associates of cones in the Inland Mountain West (Keen 1958; Hedlin 1974; Kulhavy and others 1975; Hedlin and others 1980). These include insects that feed on cones and seeds, parasitoids and predators, and species of unknown feeding habit. For example, at least 67 insect species were reared from ponderosa pine cones in New Mexico in 1964-67 (Kinzer and others 1972a). Of these, 33 species fed on cones and seeds, 43 were parasitoids, 10 were predators, and 21 were of unknown feeding habit.

There have been 22 published reports of damage by cone and seed insects in the Inland Mountain West (table 1), of which 13 were general surveys for damage to various conifers while the others were concerned with specific insects. Several surveys have reported damage as the percentage of cones attacked rather than the percentage of seeds damaged. Such surveys are difficult to interpret with regard to importance of insect pests because some insect groups, e.g., scale midges, may infest a large proportion of a cone crop but, unless large numbers are present and cones or scales are killed, cause little or no seed damage. Some of the surveys have covered many sites for only one year (Allen and Ruth 1969; Ruth and others 1980), while others have covered only one site but for several years (Barnes and others 1963; Schmid and others 1981; Jenkins 1983).

The importance of cone and seed insects in the region varies among conifers (table 1). Heavy seed losses (up to 100%) have been reported in the literature for most of the tree species for which damage surveys have been conducted, i.e., Douglas-fir, ponderosa pine, western white pine, and western larch. To date losses reported in true firs and western red cedar have been less than 30%, and lodgepole pine and western hemlock have suffered very little seed loss. However, the number of site-years for which seed losses have been reported is very limited (table 1). Even in Douglas-fir, the most intensively sampled species, 81 of the 108 site-years reported were carried out in the interior of British Columbia in 1980. The lack of adequate survey makes assessment of the general importance of cone and seed insects, as well as the relative importance of individual species, in the seed production by some conifers difficult. The seed losses (table 1) may not reflect maximum potential losses for all conifers. For example, Dewey and Jenkins (1980) reported that at one site 35% of lodgepole pine cones were infested by coneworms and scale midges. Seed losses undoubtedly occurred, but were not measured, so the loss value of 0 reported in table 1 is not a true indication of potential damage. Unpublished data from the interior of British Columbia showed that more than 75% seed loss can occur in subalpine fir. Due to difficulties in damage identification for some pests, most notably seed bug (Krugman and Koerber 1967), estimates of damage by these pests are probably conservative. The need for further surveys is obvious, especially for true firs, lodgepole pine, western larch, hemlocks, and cedars.

Seed losses vary dramatically among sites and years (table 1). For example, the percentage of seed damaged in the Cariboo Region of British Columbia in 1979 varied from less than 1% to 75% for spruce at 23 sites and from 13 to 100% for Douglas-fir at 19 sites (Allen and Ruth 1979). Variation at individual sites is largely due to the irregular fluctuations in cone crop size (Mattson 1971; Forcella 1978, 1980; Miller and others 1984). When large cone crops are preceded by light or nil crops, the size of insect populations is limited so that large crops usually suffer low levels of insect damage. Where large cone crops occur closely together losses are more severe. For example, a

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Table 1.--Cone and seed insect damage reported from the Inland Mountain West and estimated seed losses

Tree species	Surveys	Number of site-years	Range seed loss (%)
Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco)	Clark and others 1963*; Dewey 1972*; Allen and Ruth 1979; Dewey and Jenkins 1979*,1980*,1982*; Ruth and others 1980; Shearer 1984	108	0-100
Grand fir (Abies grandis (Dougl.) Lindl.)	Pfister and Woolwine 1963*; Kulhavy and Schenk 1976a*, b; Dewey and Jenkins 1980*, 1982*	30	0-19
Subalpine fir (Abies lasiocarpa (Hook.) Nutt.)	Kulhavy and others 1976; Dewey and Jenkins 1982*	1	29
Western larch (Larix occidentalis Nutt.)	Dewey and Jenkins 1980*, 1982*, Ruth and others 1980; Shearer 1984	10	0-40
Spruces (Picea engelmanni Parry) P. glauca (Moench) Voss)	Hedlin 1973; Allen and Ruth 1979; Ruth and others 1980; Schmid and others 1981; Dewey and Jenkins 1982*	40	4-100
Lodgepole pine (Pinus contorta Dougl.)	Dewey and Jenkins 1979*; 1980*; Ruth and others 1980	5	0
Pinyon pine (Pinus edulis Engelm. P. monophylla Torr. & Frém.)	Forcella 1978+, 1979+	14	<5-90
Ponderosa pine (Pinus ponderosa Laws)	Kinzer and others 1972a; Dale and Schenk 1978+; Dewey and Jenkins 1979*, 1980*, 1982*; Ruth and others 1980	40	<1-100
Western white pine (Pinus monticola Dougl.)	Barnes and others 1962+; Williamson and others others 1966+; Schenk and Goyer 1967; Dewey and Jenkins 1980*, 1982*; Jenkins 1983+	16	5-98
Western red cedar (Tsuga heterophylla (Raf.) Sarg.)	Ruth and others 1980	2	0-20
Western hemlock (Thuja plicata Donn)	Ruth and others 1980	1	2

* Damage reported as percentage of cones infested only, seed losses not reported.

\+ Seed loss can be estimated from the percentage of cones infested for pests that kill whole cones, e.g., Conophthorus spp.

very heavy crop of Douglas-fir cones occurred around Keremeos, British Columbia, in 1983. Most of the Douglas-fir cone moth (major pest) population remained in diapause in 1984 when a very light crop was produced. The moderate 1985 cone crop was heavily infested by the moth.

Stand density may affect seed loss and pest complex. Seed losses are higher in less dense stands in western white pine (Barnes and others 1961; Schenk and Goyer 1967). In ponderosa pine, cone beetle is more damaging in open stands whereas seed moth is more prevalent in dense stands (Dale and Schenk 1978).

Table 2.--Most damaging cone and seed insects associated with conifers in the Inland Mountain West

Conifer	Pest species no.[1]																												
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Douglas-fir									*					*	*								*			*		*	
Grand fir					*	*		*	*			*	*			*							*						
Subalpine fir						*		*			*					*							*						
White fir					*	*		*				*	*			*	*						*						
Western larch									*																			*	*
Spruces				*																*			*				*		
Pinyon pine		*																			*			*					
Ponderosa pine	*		*						*	*								*	*			*	*		*				
Western white pine			*						*														*						
Western red cedar							*																						

[1] See table 3 for species identification.

THE PESTS

Pest Species

Only a few insect species that feed on cones and seeds of each conifer are significant pests. Based on the damage surveys, as well as other sources (Keen 1958; Hedlin 1974; Hedlin and others 1980), the important pests on conifers in the Inland Mountain West are listed in tables 2 and 3. Cone and seed insect pests represent a wide variety of insect groups, each with its own biological characteristics. Not all pests have been identified, e.g. the most damaging insects on western larch, a wooly aphid and a scale midge (Shearer 1984).

Since most pest species are host species--or genus-specific--each conifer has its own specific complex of pests. Notable exceptions are the fir coneworm, western conifer seed bug, and western budworm. The relative importance of each pest varies throughout host range. For example, spruce seed moth and spruce cone maggot occur throughout the range of spruces in the region but the moth is most damaging in the south and the maggot in the north. Ponderosa pine cone weevil occurs sporadically within the range of its host but has done significant damage at some sites (Bodenham and others 1976). The complex of pests attacking a conifer should therefore be determined at each cone and seed production site.

Insects also damage pollen cones (Dale and Schenk 1979; Hedlin and others 1980) but apparently do not reduce pollen availability.

Pest Biology

The bionomics of most of the economically important cone and seed insects are known to some extent (table 4) and are summarized elsewhere (Hedlin and others 1980). All species, except the seed bug, complete their feeding over one summer. The seed bugs feed as nymphs and young adults over one summer and as mature adults over the next summer. Aspects of biology that are significant considerations in the development of pest management systems (table 5) include stage(s) of cone attacked and damaged, methods of mate and host location, rates of survival, amount of damage per insect, location of insects at cone harvest, and capacity for prolonged diapause.

Stage(s) of cone attacked and damaged determine the timing of insecticide applications. Female cone beetles girdle and kill conelets prior to oviposition so an insecticide should be applied when females are active. Damage by seed chalcids is done by larvae but, because chalcid larvae are protected inside conelets, an insecticide should be applied at the time of oviposition to kill adult wasps. Many pests such as cone moths, cone maggots, and some seed moths, oviposit on open strobili but damage occurs after egg hatch. Against these insects, insecticides may be applied as larvicides when the conelets have closed and are turning down or as adulticides when strobili are open to receive pollen.

Knowledge of survival rates and amount of damage per insect allows for development of damage prediction systems based on counts of an insect stage, notably eggs, that occurs prior to damage. This has been done for Douglas-fir cone gall midge (Miller 1984).

Identification of cues used in mate and host location may provide tools useful in population monitoring. The utilization of pheromones in

Table 3.--Insect pests of cones and seeds in the Inland Mountain West, their common names and species number in table 2

Insect	Common name	Species number
Coleoptera: Curculionidae		
Conotrachelus neomexicanus Fall	pine cone weevil	1
Scolytidae		
Conophthorus edulis Hopkins	pinyon cone beetle	2
C. ponderosae Hopkins	ponderosa pine cone beetle	3
Diptera: Anthomyiidae		
Lasiomma anthracina (Czerny)	spruce cone maggot	4
L. abietis (Huckett)	fir cone maggot	5
Cecidomyiidae		
Dasyneura abiesemia Foote	fir seed midge	6
Mayetiola thujae (Hedlin)	western redcedar cone midge	7
Lonchaeidae		
Earomyia abietum McAlpine	fir seed maggot	8
Hemiptera: Coreidae		
Leptoglossus occidentalis Heidemann	western conifer seed bug	9
Hymenoptera: Torymidae		
Megastigmus albifrons Walker	ponderosa pine seed chalcid	10
M. lasiocarpae Crosby	-	11
M. pinus Parfitt	fir seed chalcid	12
M. rafni Hoffmeyer	-	13
M. spermotrophus Wachtl	Douglas-fir seed chalcid	14
Lepidoptera: Olethreutidae		
Barbara colfaxiana (Kearfott)	Douglas-fir cone moth	15
Barbara sp.	fir cone moth	16
Cydia bracteatana (Fernald)	fir seed moth	17
C. miscitata (Heinrich)	-	18
C. piperana (Kearfott)	ponderosa pine seedworm	19
C. strobilella (L.)	spruce seed moth	20
Eucosma bobana Kearfott	pinyon cone borer	21
E. rescissoriana Heinrich	lodgepole pine cone borer	22
Pyralidae		
Dioryctria abietivorella (Grote)	fir coneworm	23
D. albovittella (Hulst)	-	24
D. aurenticella (Grote)	ponderosa pine coneworm	25
D. pseudotsugae Munroe	-	26
D. reniculelloides Mutuura & Munroe	spruce coneworm	27
Tortricidae		
Choristoneura occidentalis Freeman	western spruce budworm	28
Unidentified species		29

mating behavior occurs in many cone and seed insects. Sex attractants have been identified for several Inland Mountain West insects, namely: Cydia piperana, Eucosma bobana, E. ponderosae, E. recissoriana, Dioryctria pseudotsugella and Barbara ulteriorana (Sartwell and others 1984), Barbara colfaxiana (Hedlin and others 1983), and Cydia strobilella (Roelofs and Brown 1982; Booij and Voerman 1984). Pests known to or suspected of using pheromones but for which sex attractants have not yet been identified include Conophthorus ponderosae and Leptoglossus occidentalis (Kinzer and others 1972b; Dale and Schenk 1979).

Table 4.--Literature on bionomics of important cone and seed insects in the Inland Mountain West

Insect	Rererence[1]
Coleoptera:	
cone weevil	Bodenham and others 1976
cone beetles	Williamson and others 1966; Kinzer and others 1970, 1972a; Dale and Schenk 1979
Diptera:	
seed midge[2]	Hedlin 1967b
seed maggots[2]	Hedlin 1967b
cone maggots	Hedlin 1973
cone midge	Hedlin 1964b
Hemiptera:	
seed bug[2]	Koerber 1963
Hymenoptera:	
seed chalcids	Hussey 1955; Hedlin 1967b; Kinzer and others 1972a
Lepidoptera:	
cone moths	Hedlin 1960; Clark and others 1963; Hedlin and Ruth 1974
budworm	McKnight 1968
seed moths	Tripp 1954; Hedlin 1967a; Kinzer and others 1972; Hedlin 1973; Dale and Schenk 1979; Schmid and others 1981
coneworms[2]	McLeod and Daviault 1963; Dale and Schenk 1979
cone borer	Ollieu and Goyer 1966

[1] In addition to the detailed accounts listed, Keen (1958) gives some information on most groups.

[2] The bionomics are well known for only a few groups, but information on these groups is particularly lacking.

ısects may be attracted to cones through ɔst-produced volatiles (olfaction), vision, or ɔst likely both. Pine, spruce, and larch trobili produce unique blends of volatiles Borg-Karlson and others 1985) which insects ɔuld use in finding their host. Kinzer and thers (1972b) reported that presence of ɔnderosa pine conelet increased attraction to ıe opposite sex in both male and female ɔnophthorus ponderosae and that females were ttracted to host tree resins.

ɔwever, Mattson and others (1984) indicated ıat branch selection within a host tree during ɔne location was random in Conophthorus esinosae Hopkins, suggesting that ɔnelet-produced volatiles are of little ignificance in these scolytids. The spruce ɔne maggot uses vision, at least in part, to ɔcate strobili (Roques 1984). The role of ɔst-associated stimuli in host location by cone ıd seed insects has yet to be determined.

ısect location at cone harvest and capacity for rolonged diapause (table 5) influence size of ıfestation. In seed orchards, insects which re in cones at the time of harvest are removed ith the cones so that the insects must invade orchards each year for infestations to occur. Insects which are not in the cones at harvest will continually be on site. Damage will probably be greater where resident populations occur. Methods of monitoring, e.g. trap location, may differ between migrating and resident populations. Adult emergence can occur after diapause for two or more winters. This emergence can augment emergence of adults from the preceeding year's crop, resulting in greater damage (Hedlin 1964a).

The bionomics of some cone and seed pests are not well known (tables 4 and 5). The bionomics of all pests at a site must be known if pest management systems are to be effective.

PEST MANAGEMENT

Monitoring Pest Populations

Schedules for applying insecticides can be fixed (i.e., by calendar date or host phenology), flexible (i.e., when an important biological event, such as peak of oviposition is predicted to occur) or on a treat-as-necessary basis. Pest monitoring has no application in fixed-schedule spraying but is an important

Table 5.--Aspects of bionomics with implications for pest management and control

Insect	Host stage attacked	Damage by	Average number seeds damaged/insect	Location at cone harvest	Prolonged diapause
Coleoptera:					
cone weevil	2nd yr conelets	larva	?	duff	?
cone beetles	2nd yr conelets	adult	[1]3	cones on ground	yes
Diptera:					
seed midge	open strobili	larva	1	cone	yes
seed maggots	open strobili	larva	?	cone	yes
cone maggots	open strobili	larva	30	duff	yes
cone midge	open strobili	larva	?	cone	yes
Hemiptera:					
seed bug	all	adult	?	tree	no
Hymenoptera:					
seed chalcids	2nd yr conelets (pines) conelets[2] (others)	larva	1	cone	yes
Lepidoptera:					
cone moths	open strobili	larva	15	cone	yes
budworm	all	larva	?	tree	no
seed moths	2nd yr conelets (pines)	larva	12	cone	yes
	open strobili (others)	larva	14	cone	yes
coneworms	all (pines)	larva	[1]1	cone/?	no
	conelets[2] (others)	larva	?	?	no
cone borers	2nd yr conelets	larva	?	cone	?

[1] Number cones/insect

[2] 1 month after pollination

component in the latter two schedules. Cameron (1984) reviews the experiences with each approach in southern pine seed orchards. The main purpose of monitoring insect populations is the achievement of maximum control of the target pest with least amount of insecticide. Fixed schedule spraying is the least efficient way of utilizing insecticides and treating when necessary the most efficient because cone and seed insect numbers and damage vary dramatically among years and sites and control is not always warranted. Therefore, monitoring pest populations is desirable in most situations where control actions are contemplated.

Monitoring may consist of simply detecting pest presence through to quantification of pest populations and predicting damage. An effective monitoring system should allow for proper timing of insecticide applications and, when possible, for prediction of damage from the observed level of infestation.

Adult trapping with pheromone/sex attractant lures holds considerable potential for monitoring cone and seed insects. To date, none of the known attractants has been developed into a monitoring scheme. However, sex attractant-based monitoring systems have been developed for insect pests in deciduous fruit orchards (Madsen and others 1975; Madsen and Peters 1976; Vakenti and Madsen 1976) and it should be possible to develop similar systems for cone and seed insects, especially for use in seed orchards and seed production areas.

A potential problem in using sex attractant lures in seed orchards is trap placement. Because the insects must migrate into the orchards every year and mating probably takes place prior to migration, traps may need to be placed within or on the edge of nearby forest stands, which is sometimes a problem. Also, it is possible that not all cone and seed insects utilize pheromones in mating behavior. For example, the courtship behavior of _Megastigmus_ spp. has been observed (Hussey 1955; Orr and Borden 1983) but no mention was made of pheromones. In 1984, attempts to trap _M. pinus_ with virgin insects near Victoria, British Columbia failed.

Host attractants hold similar potential for monitoring adult populations. Host attractants have the following advantages over sex attractants: i) they should be attractive to

everal species rather than being pecies-specific; ii) they should attract emales whereas in most species males are ttracted to sex attractants, and counts of emales should provide a more direct estimate of otential damage; and iii) they could be used in eed orchards, thus avoiding the potential roblem of trap location associated with sex ttractant traps. Visual traps which simulate osts and which also emit host volatiles are sed to monitor populations of some pests in eciduous fruit orchards (Prokopy and Hauschid 979; Reissig and Tette 1979) and such traps may e best for cone and seed insects.

lacklight traps have been used to monitor oneworm populations in southern pine seed rchards (McLeod and Yearian 1979, 1982). They re most effective for moths; many other nsects, including seed bugs (Yates 1973), are ot attracted. Since these traps are not elective they can catch large numbers of many on-target lepidopteran species, resulting in ifficulties in specimen identification. They re not considered practical for operational use n southern pine seed orchards (Cameron 1984).

ampling schemes for quantifying Douglas-fir one moth egg populations and determining the eed for applications of systemic insecticide re currently being developed in British olumbia. Similar schemes are needed for opulations of other pests, especially for nsects which can be monitored prior to ccurrence of damage, such as those which viposit on open strobili. The current lack of onitoring schemes is a major gap in the evelopment of pest management systems.

ontrol Techniques

urrently, insecticides are the only practical echnique for controlling cone and seed insect opulations or damage. However, in seed rchards, certain cultural practices can reduce eed losses. For instance, annual removal of nsect populations in harvested cones, including nwanted cones on rootstocks or crops too small o manage for seed production, should reduce nsect damage. Leaving cones in orchards allows esident insect populations to build up and esults in heavier seed losses. This has appened in coastal Douglas-fir seed orchards Miller 1984). Similarly, cone-beetle infested ones lying on the ground should be removed from rchards. Delaying reproductive bud burst hrough overhead misting with cold water for educing pollen contamination may also reduce nsect damage in some years (Miller 1983b). owever, the effects of this technique on damage y insect pests in the Inland Mountain West have ot been evaluated.

nsecticides. - Many contact and systemic nsecticides have been tested for cone and seed nsect control but only a few are effective. or example, of 26 insecticides tested on ouglas-fir cones only 11 reduced insect opulations or damage by 90% or more (Miller 1980). Because of timing of sprays, contact insecticides can only be used as preventatives whereas systemic insecticides can be used after the need for insecticide application has been established, at least for insects that oviposit on open strobili. Systemic insecticides have a further advantage in the number of ways that they can be applied. Systemics can be applied as sprays, injections, paint-ons, or incorporated into the soil whereas contacts can only be applied as sprays.

Insecticides effective against inportant cone and seed insects in the Inland Mountain West are listed in table 6. Significant increases in seed production after insecticide application have also been reported by Stipe and Green (1981) and Reardon and others (1984). There are few reports of insecticide efficacy against pests on conifers other than Douglas-fir, and even against some pests on Douglas-fir, such as seed bug. In Canada, azinphosmethyl and dimethoate are registered for use on Douglas-fir (Agriculture Canada 1982) and dimethoate is currently being registered for spruce cone and seed insects. In the United States, azinphosmethyl, dimethoate, Pydrin® and oxydemetonmethyl were registered for specific uses against Douglas-fir cone and seed insects (Overhulser and Sandquist 1985) and fenvalerate is registered for use on western white pine. Obviously options in pest control are limited.

Research elsewhere on cone and seed pest control may be applicable in the Inland Mountain West. For example, insecticides have been evaluated against seed bug and coneworms of southern pines (DeBarr and Nord 1978; DeBarr and Fedde 1980; Nord and DeBarr 1983; Nord and others 1984) which are related to the species in the West. These evaluations in the south provide a list of most suitable candidate insecticides for trial against western species.

Efficacy of various available application methods has not always been consistent, especially for aerial sprays and injections. Aerial sprays have sometimes been more than 90% effective (Miller and Hutcheson 1981) but have also been totally ineffective (Johnson and Winjum 1960; Johnson 1963). These "one-shot" trials have not been attempts at systematic technique development. In southern pine seed orchards, frequency of aerial applications is increasing (Barber 1984), suggesting satisfactory results are being obtained. Injections have been tested for effectiveness in reducing insect damage in Douglas-fir (Koerber and Markin 1984; Reardon and others 1984), spruce (Fogal and Lopushanski 1984) and southern pines (Merkel and DeBarr 1971), but again the results have ranged from excellent to poor. Two causes of the variation are poor uptake of the insecticide by individual trees and uneven distribution of insecticides within the tree crown (Koerber and Markin 1984). With proper timing, ground-based sprays have generally resulted in consistent effective control, provided sprays are not affected by rain (Miller

1983a; Nord and others 1984). However, ground-based sprays are limited by tree height and size of the area being treated. Incorporation of insecticides into soil has been effective in southern pine seed orchards (DeBarr 1978) and requires only one application per year, compared to several sprays for coneworm and seed bug control (Neel 1980). As with injections, level of control has varied (Nord and others 1979). Soil incorporation trials have not been reported from the West. More technique evaluation and development, as occurred in southern pine seed orchards (reviewed by Barber (1984)), is needed in our region if consistent and effective control of cone and seed insects is to be achieved in the future.

Not all application methods are equally effective against all pests. Soil incorporation of carbofuran controlled several pests on eastern white pine but not seed chalcid (DeBarr and others 1982). Likewise, timing of application for one pest may not control another. For example, injecting or spraying Douglas-fir when strobili were open or turning down controlled Douglas-fir cone gall midge and cone moth but not seed chalcid (Koerber and Markin 1984; Miller unpubl.). These points should be remembered when developing pest management systems.

The most practical method of insecticide application will vary with the type of stand to be treated. Protection of crops in forests is only practical through aerial applications because of tree size and variable terrain. Protection of seed crops on plus trees, being individual trees within forest stands, is possible through injecting insecticide and aerial spraying. In seed production areas (depending on terrain) and especially in seed orchards, all methods of application are possible. Provided the trees are not too tall and the area being treated is small, ground-based sprays or soil incorporations are likely the most cost effective. Otherwise, onl aerial applications are practical. Injections are too expensive and time-consuming to be used in the treatment of whole orchards or seed production areas.

In some conifers, pest control can be relativel simple; a single application of systemic

Table 6.--Insecticides demonstrated to be 90% effective against insect pests of cones and seeds in the Inland Mountain West

Tree	Insecticide type	Insecticide name	Application method	Pest	Reference
Douglas-fir	contact	azinphosmethyl	spray	cone moth	Johnson and Winjum (196
			spray	coneworm	Cade (1977)
		DDT	spray	cone moth	Rudinsky (1955)
			spray	seed chalcid	Rudinsky (1955)
		lindane	spray	coneworm	Cade (1977)
		malathion	spray	seed chalcid	Stoakley (1973)
	systemic	acephate	spray	coneworm	Cade (1977)
		dicrotophos	spray	cone moth	Meso (1975)
			injection	cone moth	Meso (1975)
		carbofuran	spray	coneworm	Cade (1977)
		dimethoate	spray	cone moth	Hedlin (1966)
			spray	coneworm	Cade (1977)
			spray	seed chalcid	Hedlin (1966)
			injection	cone moth	Meso (1975)
			injection	seed chalcid	Meso (1975)
		fenitrothion	spray	seed chalcid	Hedlin (1966)
		oxydemetonmethyl	spray	cone moth	Meso (1975)
			injection	cone moth	Schenk and others (1967
			injection	cone moth	Koerber and Markin (198
		phorate	spray	cone moth	Johnson and Winjum (196
spruce	systemic	dimethoate	spray	cone maggot	Hedlin (1973)
		oxydemetonmethyl	spray	cone maggot	Hedlin (1973)
			spray	seed moth	Hedlin (1973)
			injection	seed moth	Fogal and Lopushanski (84
			injection	cone maggot	Fogal and Lopushanski (84
		dicrotophos	injection	seed moth	Fogal and Lopushanski (84
			injection	cone maggot	Fogal and Lopushanski (84
western white pine	contact	permethrin	spray	cone beetle	Shea and others (1984)

ısecticide controls both major seed pests (seed)th and cone maggot) of spruce (Hedlin 1973). ı conifers attacked by only one pest species, ıch as western red cedar and western white pine : some sites, control should be relatively ısy. In other conifers which are attacked by ..fferent pests at different stages of cone ›velopment, e.g. Douglas-fir and ponderosa ..ne, or by pests that initiate attacks on cones ıd seeds over several weeks or months, e.g.)neworms and seed bug, control of damage may be)re difficult to achieve consistently and may ›quire multiple insecticide applications.

ıological control.--The prospects for ıological control appear limited, even though)me insects, such as Douglas-fir cone moth Hedlin 1960), suffer heavy losses to natural ıemies because pest damage is usually completed :ior to pest death caused by these mortality ıctors. Entomophagous fungi may provide an lternative to chemical insecticides (Timonin ıd others 1980) but further research is needed ı evaluating these pathogens and in application ›chniques. Research in the southern U.S. has ıown that Bacillus thuringiensis is another)tential control agent for coneworms (McLeod ıd others 1982).

ı summary, seed crops protected from one pest ıy suffer damage by other pests, or damage may › caused by a less important pest because no ısecticide applications were made due to low ›vels of infestation by key pests (Cameron)84; Miller 1984). Obviously pest management /stems should be developed to include all pests ssociated with a conifer. Considerably more ›search is needed before pest management /stems will be available for cone and seed ›sts in the Inland Mountain West.

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INSECTS DESTRUCTIVE TO PONDEROSA PINE CONE CROPS IN NORTHERN ARIZONA

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ABSTRACT: The insect damage to the 1984 ponderosa pine, Pinus ponderosa, cone and seed crop is reported. Three cone infesting insects (Dioryctria auranticella, Conophthorus ponderosae, Conotrachelus neomexicana) and two seed infesting insects (Cydia piperana, Megastigmus albifrons) were responsible for as much as 100 percent reduction in seed yield. Impact of seed and cone insect damage in 1984 is compared to previous estimates of insect damage. An economic comparison of the ponderosa pine seed value with and without insect damage is presented.

INTRODUCTION

Cone and seed insects are one of the most important biotic factors affecting seed production and thereby regeneration of ponderosa pine, Pinus ponderosa Dougl. ex Laws., in the Southwest. Studies in California (Koerber 1967), New Mexico (Kinzer and others 1972), Colorado (Bodenham 1973), and Arizona (Schmid and others 1984, unpublished manuscripts) indicate four insect species as the major damaging agents on ponderosa pine. These include the ponderosa pine coneworm (Dioryctria auranticella (Grote) (Lepidoptera: Pyralidae)), the ponderosa pine cone beetle (Conophthorus ponderosae Hopkins (Coleoptera: Scolytidae)), the ponderosa pine seedworm (Cydia piperana (Kearfott) (Lepidoptera: Olethreutidae)), and the ponderosa pine seed chalcid (Megastigmus albifrons Walker (Hymenoptera: Torymidae)). Other less prevalent cone and seed insects are the cone midge (Thomasiniana sp.), the pine cone weevil (Conotrachelus neomexicana Fall (Coleoptera: Curculionidae)), and the western conifer seed bug (Leptoglossus occidentalis Heidemann (Hemiptera: Coreidae)).

The reduction of seed yield by cone and seed insects varies by location, tree, and year. Koerber (1967) reports damage from C. piperana of 37 percent in 1963 and only 9 percent the following year. Kinzer and others (1972) report an overall reduction in seed yield of 82 percent in New Mexico, with individual trees exceeding 90 percent. Schmid and others (1984) show damage by Conophthorus ponderosae, M. albifrons, and Cydia piperana in northern Arizona varies significantly between study areas and between trees within study areas. They also report no significant difference between tree crown levels. The year to year variation in ponderosa pine cone production coupled with cone and seed insect damage makes estimates of seed yield uncertain at best.

METHODS

Five study plots were selected in fall 1984 on the Coconino and Kaibab National Forests. Each plot included 10 ponderosa pine trees ranging in height from 10 m to 15 m. Twenty live and 20 dead cones were collected from each of two crown levels (uppe half and lower half). The entire live cone crop was collected from trees which produced less than 20 live cones. The collected cones were placed in labeled burlap bags and taken to the laboratory fo evaluation. The number of remaining live and dead cones on each tree was counted and recorded.

Evaluation of cone and seed damage occurred in thr steps. Dead cones were visually examined and the cause of mortality (Conophthorus ponderosae, Dioryctria auranticella, Conotrachelus neomexicana, or aborted) was recorded. The second step was a scal by scale dissection of all live cones. The number of sound-appearing seeds, aborted seeds, and Cydia piperana damaged seeds were recorded. Finally, al sound-appearing seeds were x-rayed and categorized as filled, unfilled, Megastigmus albifrons damaged, and other-damaged seeds.

Cone and seed insect specimens found during the study were reared to adults for species identification. Damage was then associated with the reare specimens.

All data were subjected to analysis of variance (ANOVA, α=0.05) by crown level, plot, and trees within a plot. Data were transformed where necessary to meet the assumptions of homogeneity of variance. The Student-Newman-Keuls and Least Significant Difference multiple range tests were usec to determine where differences occurred.

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RESULTS

Five insect species were found to cause significant damage to the ponderosa pine cone and seed crop in 1984. A brief description of each insect species and the damage it causes is given below.

Cone Insects

Damage to cones by the ponderosa pine coneworm, *Dioryctria auranticella*, ranged from 19 percent to 71 percent of the total cones produced per tree. This insect species caused the heaviest damage to the cone crops in our study areas.

Dioryctria auranticella feeds on seeds and scale tissue of ponderosa pine and knobcone pine during the larval stage (Hedlin and others 1981). The larvae enter the basal portion of the cones and bore irregular shaped feeding cavities within the cone. Reddish-brown frass and webbing fill the large cavities (fig. 1). Pupation occurs within the cavity; the pupal stage lasts from 10 to 14 days. Adults emerge, mate, and lay eggs in July. Little is known of the lifecycle from July until the larvae appear in the cones the following spring. Entire cones are usually killed by *D. auranticella* infestation; partially killed cones become distorted and do not open.

Figure 1.--*Dioryctria auranticella* larva feeding on seeds and scales of ponderosa pine. Frass and webbing fill the feeding cavities.

In this study damage to cones by the ponderosa pine cone beetle, *Conophthorus ponderosae*, ranged from 2 percent to 19 percent per tree. The adult female beetle kills cones by severing the conductive tissue of the cone stalk (Hedlin and others 1981). A pitch tube usually marks the point where the adult enters the cone in early summer to construct a gallery and lay eggs (fig. 2). The dead cones turn brown and may remain on the tree or drop to the ground. Larvae feed randomly in the cone where they complete development in approximately one month, pupate, and emerge as adults. The adults may overwinter in the dead cones, or enter shoots or conelets where they feed and overwinter. In Arizona very few adults have been found overwintering in cones. No viable seed is produced by cones infested with *C. ponderosae*.

Figure 2.--A pitch tube at the base of a ponderosa pine cone marks the place where an adult *Conophthorus ponderosae* entered the cone.

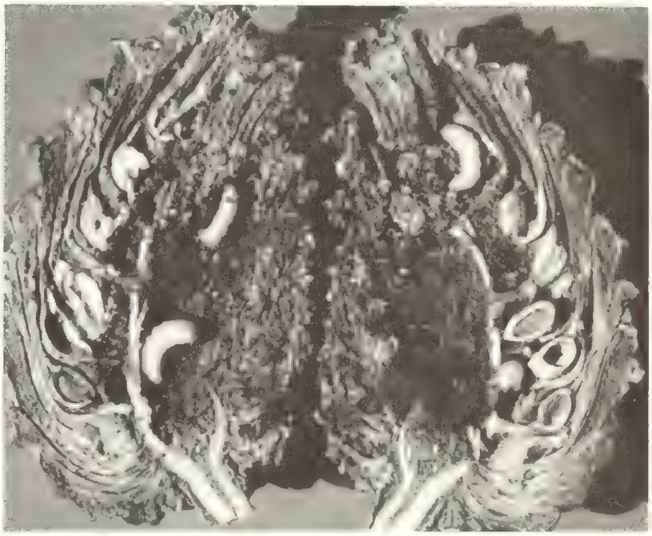

Figure 3.--Larvae of *Conotrachelus neomexicana* feeding on scales and seeds of a developing ponderosa cone.

Cone damage by the pine cone weevil, *Conotrachelus neomexicana*, was relatively light at our study plots when compared to *D. auranticella* and *Conophthorus ponderosae*. Damage ranged from 7 percent to 14 percent of the cone crop per tree.

Larvae of *C. neomexicana* feed indiscriminately on the scales and seeds of developing cones (Bodenham 1973) (fig. 3). The pinkish-white to yellowish-white larvae feed for four to six weeks and, after being stimulated by rain, mature larvae chew exit holes through the outer shell of the cone and drop to the ground. They then burrow into the soil and pupate. Adults are formed in eight to 12 days but remain in the pupal cell for a few days while they darken and harden. The adults make their way to the surface, feed on shoots for a brief period, and burrow into the litter where they overwinter.

Seed Insects

Damage to seeds by the ponderosa pine seedworm, *Cydia piperana*, ranged from 1 percent to 11 percent of seeds per cone in this study. The

larvae consume the entire contents of each seed as they migrate from one seed to another within the cone (Hedlin and others 1981). Damaged seeds are filled with frass; seed pairs may be fused together by silk-lined tunnels of frass. Larvae burrow exit tunnels through mined seeds and then retreat to the cone axis where they overwinter (fig. 4).

Figure 4.--A mature larva of Cydia piperana in the cone axis. Larvae migrate from seed to seed, consuming the entire contents of each seed they encounter.

Pupation occurs in the spring and, after approximately two weeks, the pupae wriggle halfway through the exit hole and the adult moth emerges. One to three larvae may inhabit a single cone and may destroy a significant amount of the seed produced.

An average 53 percent of seeds which appeared to be normally developed were found to contain larvae of the ponderosa pine seed chalcid, Megastigmus albifrons, when x-rayed. Overall, 7 percent of the total seed production per cone was damaged by M. albifrons in this study.

The larvae of M. albifrons completely consume the contents of ponderosa pine seeds (Hedlin and others 1981). No external evidence of seed infestation is apparent until adults emerge in spring. Female adults oviposit through the cone scale into the immature seed. Only one larva completes development in each seed. The presence of larvae can be detected by x-raying the seed (fig. 5). Pupation occurs in the seed; adults emerge by chewing exit holes through the seed coat.

Comparison of Two Studies in Northern Arizona

Two studies of cone and seed insects in northern Arizona report the incidence of damage to ponderosa pine cone and seed production. Schmid and others (1984) reported findings for 10 locations; we report findings for five locations, three of which were studied in 1982 by Schmid and others (1984). These three plots are used for comparison of cone and seed insect damage.

Both studies report no statistically significant difference in damage between crown levels (middle and lower, Schmid and others (1984), upper and low this study). Differences in damage caused by C. pondersae, Cydia piperana, and M. albifrons were significant between plots and among trees within plots in both studies. However, Schmid and others (1984) reported no difference in damage by D. auranticella between plots or trees within plots in 1982, while we did find these differences in 1984. Table 1 compares the incidence of D. auranticella and Conophthorus ponderosae at the US Highway 89, Deadman Flat, and Williams 345 Road plots. The incidence of D. auranticella increased dramatically in all plots from 1982 to 1984. Damage to cones by C. ponderosae decreased at the US Highway 89 and Deadman Flat plots but increased substantially at the Williams 354 Road plot. The common factor between the data is an apparent displacement of one species by the other in each year. Schmid and others (1984) did not report damage by Conotrachelus neomexicana

Figure 5.--Larva of Megastigmus albifrons inside a ponderosa pine seed. Seeds must be x-rayed to detect the presence of M. albifrons because no external evidence of infestation is apparent.

A comparison of seed damage between 1982 and 1984 showed the relative effect of seed insects and environmental factors that influence viable seed production (table 2). The percentage of sound and hollow seed decreased substantially at the Deadman

Table 1.--Comparison of the percentage of dead cones killed by Dioryctria auranticella and Conophthorus ponderosae at three plots in northern Arizona

	D. auranticella		C. ponderosae	
Plot	1982[1]	1984[2]	1982	1984
US Hwy 89	1	80	39	10
Deadman Flat	1	78	15	9
Williams 354 Road	0	55	0	32
X̄	<1	71	18	17

[1]Data for 1982 from Schmid and others (1984).
[2]Data for 1984 from this study.

Flat and Williams 354 Road plots; the US Highway 89 plot experienced a slight decline in these same categories. Schmid and others (1984) did not report aborted seed in their 1982 damage estimates. Perhaps aborted seeds were counted as hollow seeds or no obviously aborted seeds were found. Our study showed aborted seeds constituted 75 percent or more of the seed crop at all three study areas. If the percentage of aborted and hollow seeds are combined, the impact on total seed production in 1984 is substantial.

Comparison indicates a decrease in both C. piperana and M. albifrons in 1984. This decrease is probably due to the large percentage of aborted seeds which are unavailable for insect infestation. Of the seeds which appeared to be normally developed at the time of dissection, 45 to 67 percent were found to be infested with M. albifrons when x-rayed.

CONCLUSIONS

Damage to ponderosa pine cone and seed crops by insects is highly variable from year to year. One cause of this variation appears to be a combination of the population dynamics of the damaging insects and the size of the previous and current cone crops. If good cone crops are produced for several years and then a poor crop is produced, the insects will concentrate on the few cones and damage much of the crop. However, if several poor crops are followed by a moderate to good crop, the relatively small insect population that was supported by the poor cone crops will be dispersed and cause little damage to the large crop.

Table 3 compares the seed yield and cost per pound of seed, assuming an initial crop of 200 cones per tree. The comparison is for no insect damage and insect damage using estimates for 1982 (Schmid and others 1984) and 1984. The value of the sound seed produced per tree in 1984 is 83 times less than the value per tree if no insect damage were to occur, and 27 times less than the estimated value in 1982. The variability of the damage and value estimates between 1982 and 1984 point out the need for precise estimates of cone and seed damage prior to cone collection each year.

Table 2.--Comparison of the percentage of sound, hollow, aborted, Cydia piperana damaged, Megastigmus albifrons damaged, and other damaged seeds per cone at three locations in northern Arizona

	Sound		Hollow		Aborted		C. piperana		M. albifrons		Other	
Plot	1982[1]	1984	1982	1984	1982	1984	1982	1984	1982	1984	1982	1984
US Hwy 89	2	<1[2]	8	5	--	88	77	2	16	5	--	<1
Deadman Flat	38	<1	16	4	--	75	31	11	11	10	--	<1
Williams 354 Road	60	<1	33	7	--	84	3	1	14	6	--	<1
$\bar{X}$	33	<1	19	5	--	82	37	5	14	7	--	<1

[1] Data for 1982 from Schmid and others (1984).
[2] Percentages may not add to 100 due to rounding.

Table 3.--Comparison of the value of sound seed produced per tree for non-insect damaged and insect damaged cone crops

	No Insect Damage	Insect Damage 1982[1]	Insect Damage 1984
Initial number of cones/tree	200	200	200
% cone mortality	0	28	60
Surviving cones	200	144	80
Average number of sound seed/cone	47	21	0.9
Sound seed/tree	9,400[2]	3,024	72
Seeds/pound	11,400[3]	11,400	11,400
Pounds of sound seed/tree	0.82	0.27	0.01
Value/pound of seed	$38.00[4]	$38.00	$38.00
Value of seed/tree	$31.60	$10.26	$ 0.38

[1] Data from Schmid and others (1984).
[2] Based on U.S. Forest Service estimate of 75 percent sound seed per tree.
[3] Estimate from Schopmeyer (1974).
[4] Estimate from U.S. Forest Service.

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WESTERN SPRUCE BUDWORM IMPACT ON DOUGLAS-FIR CONE PRODUCTION

Jerald E. Dewey

ABSTRACT: The western spruce budworm is the most destructive pest of Douglas-fir cones in much of the Inland Mountain West. Budworm feed on Douglas-fir flowers and cones throughout their entire larval stage, sometimes destroying more than one cone. This paper discusses the general impact of budworm on cone production as determined from numerous surveys and evaluations, as well as a specific study conducted in 1983. In 1983, 772 cones on 14 trees were tagged and examined four times between early May and late August. The number of cones remaining in late August was approximately 60 percent of what was counted in May, and 21.6 percent of those were conspicuously injured by insects. This cone loss was attributable to all factors; however, the western spruce budworm was the single most damaging agent.

INTRODUCTION

For many years forest managers have recognized the western spruce budworm (Choristoneura occidentalis Freeman) as a severe defoliator of Douglas-fir, true fir, and spruce forests. Native to western forests, the budworm population periodically becomes epidemic over very large areas. Western spruce budworm defoliated approximately 4.2 million hectares (10.38 million acres) in the western U.S. in 1984, and another 62,000 hectares (153,202 acres) in British Columbia (Kucera and Taylor 1985).

This voracious defoliator is not widely recognized for its influence on cone and seed production. Budworm affect seed production in a number of ways. As a defoliator, they concentrate in the upper crowns of host trees. Several consecutive years of feeding will leave very thin crowns or dead tops.

Most Douglas-fir cones are produced in the upper tree crown. By topkilling potential cone-bearing trees, budworm reduce cone production. Severe defoliation may trigger a stress cone crop response in the trees, but there is uncertainty regarding the viability of seed from these cones.

Budworm reduce cone production more directly by feeding on developing flowers, cones, and reproductive buds during all stages of larval development, from emergence in the spring until pupation. Fellin (1985) reports budworm larvae become active as early as the end of April and that nearly all larvae are feeding by mid-June. Vegetative buds are usually still very tight through the month of May. But reproductive buds are swollen or may have burst by the first of May.

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OBSERVATIONS

Newly emerged larvae have three food sources: mining old needles; mining tight vegetative buds; or feeding on reproductive buds or flowers. I have observed that buds and flowers are a preferred food source. While they feed freely on developing pollen buds and male flowers, the impact of this feeding has not been well evaluated. Because most conifers produce an excess of pollen, I suspect the feeding on male buds and flowers usually does insignificant damage to Douglas-fir seed production.

Budworm larvae feeding on reproductive buds, female flowers, or small conelets generally kill them by severing the conductive tissue. This results in rapid dessication and shedding, requiring the larvae to seek new feeding sites. As a result of this feeding characteristic, the budworm is particularly damaging to cones. A single larva can completely destroy one to several cones. In contrast, many of the other cone-feeding insects may destroy only a single seed or portion of a cone.

Budworm larvae are only about 1 to 2 millimeters (.04 to .08 inches) in length when newly emerged from overwintering. As a result, budworm damage is frequently overlooked or misdiagnosed. Conelets killed by budworm are often wrongly attribubted to lack of pollination, abortion, or frost.

As cones grow in size, budworm feeding damage symptoms change. Fewer cones are killed outright. But various degrees of cone mining and surface feeding can be observed as the cones develop. This mining and surface feeding results in seeds being devoured, deformed cones that reduce seed recovery, and perhaps reduced seed viability.

PREVIOUS STUDIES

A number of studies provide information about budworm damage to seed production. In a cone and seed insect survey in Montana and Yellowstone National Park, Dewey (1970) found that budworm

damaged or destroyed up to 71 percent of the Douglas-fir cones. Stipe and Hard (1980), in a light cone-crop year coupled with a large budworm population, found a peak of 8.2 early instar larvae per cone. The result was shedding of most of the developing cones and loss of the entire seed crop by the end of the season.

A survey of Idaho and Montana seed production areas revealed budworm are Douglas-fir cones' most damaging pest. Damage was greatest where the defoliator was at epidemic levels (Dewey and Jenkins 1982). Chrisman and others (1983), examining Montana Douglas-fir cone production in 12 stands with varying levels of defoliation, found that average cone production is usually higher in stands with little or no defoliation. That is, western spruce budworm infestations reduce cone production.

1983 MONTANA STUDY

A study, designed to measure the amount of Douglas-fir cone loss from flowering to cone maturity, was conducted in 1983 in a budworm-infested Douglas-fir stand near Frenchtown, MT. Fourteen flowering Douglas-fir trees, ranging from 8.5 (27.9 feet) to 13.7 meters (44.9 feet) in height, were selected for monitoring. Four cone-bearing upper crown branches were tagged on each tree. The entire cone complement per branch was counted four times between May 4 and August 31. Table 1 presents the results of cone counts at various dates.

Table 1.--Cone counts in 14 Douglas-fir trees near Frenchtown, MT, 1983

Tree number	Date				Percent loss
	5/4	6/1	7/25	8/31	
1	102	108	97	98	9
2	75	69	52	20	73
3	48	54	39	7	87
4	61	62	47	35	44
5	84	95	77	77	19
6	57	55	51	42	26
7	66	62	42	35	47
8	38	40	36	31	22
9	43	40	34	27	37
10	44	43	17	16	64
11	21	21	15	12	43
12	43	47	34	31	34
13	37	34	28	25	32
14	39	42	16	9	79
Total or Average	758	772	585	465	40

Because the conelets were only about 10 to 20 millimeters (.4 to .8 inches) long at the time of the first count, a number of them were not seen. On one tree (#5), 11 more cones were noted on the second count than on the first. As reported by Stipe and Hard (1980), considerable cone loss can occur to the small developing conelets in May. Hence more cones were apparently missed on the first count than indicated by the second count.

Agents other than budworm can cause a decline in cone numbers between May and September. While winds, hail, and rain can dislodge cones from trees, there was no evidence that these elements contributed to the reduced cone numbers during the 1983 study. Squirrels often begin cone cutting prior to August 31, but a significant amount of cone cutting had not occurred at this location prior to the final count. The cone counts in table 1 do not reflect cone conditions, just cone presence.

At the time of the last count, all cones on the survey branches were collected, taken to the laboratory, rated for insect damage, and weighed. Cones weighed an average of 4.4 grams (.16 ounces) per cone, compared to 8.8 grams (.31 ounces) for cones collected at the same time from a nearby forest where an insecticide had been used to control pests (Stipe and Dewey 1985). There was visual evidence of insect damage on 21.6 percent of the cones collected in the study.

SUMMARY AND CONCLUSIONS

Forty percent of the 772 Douglas-fir cones present on June 1 had fallen from the trees by August 31. Of the remaining 465 cones, 21.6 percent had obvious symptoms of the insect damage Although actual counts of the pest complex were not made, the western spruce budworm was responsible for most of the damage. The study year, 1983, was a moderate to good cone-crop year, and a year with a light (nondefoliating level) budworm population.

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PROTECTION OF BLISTER RUST-RESISTANT WESTERN WHITE PINE CONES FROM INSECT DAMAGE WITH PERMETHRIN AND FENVALERATE

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ABSTRACT: Production of seed from blister rust-resistant western white pine in northern Idaho has been severely reduced by the mountain pine cone beetle and the fir coneworm. In 1981 and 1984, insecticide treatments to control these insects to maximize seed production were evaluated in Idaho. At one test site, Sandpoint, 0.03 pct. permethrin significantly reduced loss of cones to the mountain pine cone beetle; however, 0.06 pct. permethrin was more cost effective. At the other test site, Moscow, the fir coneworm infested 46.6 pct. of the untreated cones, significantly more than 13.6 pct. in the single application of 0.025 pct. fenvalerate. A double application of fenvalerate increased seed yield significantly from 31.3 to 56.0 seeds/cone when compared to the untreated check. A third application of fenvalerate was apparently unnecessary.

INTRODUCTION

Western white pine (Pinus monticola Douglas) is one of the more valuable species in the northern Rocky Mountains. However, the introduction of the pathogenic fungus Cronartium ribicola Fischer to the United States from Europe in the early 1900's nearly eliminated western white pine (Haig and others 1941). To preserve this species for timber, the USDA Forest Service started a breeding program to select for resistance to this disease (Bingham 1983).

Recently, the production of blister rust-resistant seed from western white pine in seed orchards has been severely reduced in Idaho because of periodic infestations of the mountain pine cone beetle Conophthorus ponderosae Hopkins (=C. monticolae) at the Sandpoint (Idaho) Seed Orchard (Jenkins 1982; Shea and others 1984) and the fir coneworm Dioryctria abietivorella (Grote) at the Moscow (Idaho) Arboretum (Haverty and others 1985; Shea 1985). The western conifer seed bug Leptoglossus occidentalis Heidemann and the lodgepole cone moth Eucosma rescissoriana Heinrich have been observed in the Moscow Arboretum; however, we have not yet associated any significant damage with these insects.

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The life history of C. ponderosae with respect to the phenology of white pine cones has been described (Williamson and others 1966). White pine cones require about 15 months to reach maturity (Owens and Molder 1977). In early spring, as second-year cones begin to elongate, adult cone beetles emerge from overwintering sites within old cones. Female beetles initiate attack and bore into the young cones. They rapidly girdle the axis of the cone, thereby severing the conductive tissue and killing the cone. Adult females may attack up to four cones, depositing a maximum of 100 eggs. Normally, however, only 4 to 8 adults emerge from an infested cone (Jenkins 1982). The rapid attack and subsequent mortality before the cones are half-grown make successful control difficult (Furniss and Carolin 1977).

The fir coneworm is a transcontinental species that attacks cones of many conifer species. It also mines in the buds, shoots, and trunks of conifers. Its life history is variable and not well known. Apparently, in Moscow, larvae pupate in cocoons on the ground in August and September and emerge as moths in June. Eggs are laid soon after emergence, and larvae feed from June to August or September. Larvae mine the inside of cones but also crawl on the outside throughout cone development (Furniss and Carolin 1977; Hedlin and others 1980). Feeding throughout the cone development period could necessitate multiple insecticide applications.

This paper reports the results of experiments conducted in Idaho in 1981 and 1984 to evaluate single and multiple, high-volume ground applications of two insecticides--permethrin and fenvalerate--for protection of cones of blister rust-resistant western white pine. Our objective was to protect the cone crop from the major pest at two test sites (Sandpoint and Moscow) that attack cones during the second year of cone development.

MATERIALS AND METHODS

The insecticides selected were chosen on the basis of human safety and efficacy against C. ponderosae (Haverty and Wood 1981) or Dioryctria spp. and Leptoglossus corculus (Say)(Nord and others 1984).

Sandpoint-Conophthorus

The study site was the Sandpoint Seed Orchard. In 1981, the 17.3-acre (7.0-ha) orchard contained 800 grafts of 21-year-old western white pine. Trees ranged in height from approximately 15 to 45 ft (5

o 15 m). Permethrin (Pounce) was sprayed in pril 1981. Ten trees between 20 and 45 ft (7 and 5 m) tall were randomly assigned to each of seven reatments. Ramets were from three clones with imilar susceptibility to C. ponderosae attack Jenkins 1982). Trees next to a previously selec-ed tree or in a previously designated buffer zone ere not used. The seven treatments consisted of n untreated check, and 0.03, 0.06 and 0.12 pct. ermethrin in water applied once, the same concen-rations applied again 14 days later. Trees were prayed between 0500 and 0930 within a 2-day eriod with a Bean hydraulic sprayer mounted on a railer. The sprayer was calibrated to deliver pproximately 5 gallons (18.9 liters) per tree ithin 48 seconds. Mixing was done just before pplication and all trees within a treatment were reated consecutively. The order of treatment ithin any morning was random.

wenty-one days following the second application nd after all attacks had occurred, all cones on ll trees were inspected and counted as infested s. noninfested. Because timing is critical to rotection of the cone crop, five screened cages, ach with 50 infested cones collected in the rchard or from the surrounding area, were placed nroughout the orchard. Spraying began 1 day fter the first beetle emerged. Treatments were nalyzed by pairwise tests of differences with a 2 2 contingency table (infested vs. noninfested s. treatment) and a chi-square statistic at α = .01.

revious work in the orchard indicated a high robability that the beetle population would be ow in 1981 (Jenkins 1982). Because of concern nat insufficient attacks would not allow an dequate test of the insecticide, beetles were ollected elsewhere and placed throughout the rchard. Infested cones containing overwintering eetles were collected in and around Sandpoint, nd held until the trees were treated. Immedi-tely after spraying, 15 infested cones were laced under test trees (including checks) to nsure adequate attack.

oscow-Dioryctria

ne Moscow seed orchard is rectangular in shape nd covers approximately 12 acres (4.9 ha) on the astern edge of the University of Idaho campus. ur study area comprised the northeast quarter of ne seed orchard and had approximately 340 P. onticola of cone-bearing age. Only trees with an nitial cone crop of $\geq$ 20 second-year cones were sed. The remainder of the seed orchard was eparated from the study area by a draw at least) ft (20 m) wide. To protect the majority of the one crop in the seed orchard from seed-destroying nsects, this area was treated three times (once ach in May, June, and July) with fenvalerate pplied aerially at a rate of 0.75 lb AI/acre 0.84 kg AI/ha) delivered in 10 gallons of water 93.5 liter/ha). The draw served as a clearly isible buffer to guide the helicopter pilot so hat the insecticide would not drift into the tudy area. Insecticide drift was monitored uring each spray application with water-sensitive pray deposit cards. No drift was detected, and the study area was assumed to be free of insec-ticidal contamination from the adjacent control operation.

Fenvalerate (Pydrin Insecticide 2.4 EC) was diluted in water to a concentration of 0.025 pct. (wt/wt) and applied with a trailer-mounted sprayer. Mixing was done just before applica-tion. The tank mixture was applied to near the point of runoff with an FMC Bean hydraulic pumper using a hand-operated gun. Trees were sprayed in the early morning and late evening when wind was minimal to avoid contamination of adjacent trees. Between applications, spray equipment was cleaned and rinsed with Nutra Sol.

Treatments were done on three dates in 1984: 9 May, 13 June, and 18 July. Since exact phenolo-gies of the three insect pests were unknown, the application schedules were modified after the procedure of Nord and others (1984) to be approx-imately 30 days apart. Pheromone traps baited with candidate E. recissoriana pheromone were distributed diagonally across the orchard at about 6 ft (2 m) above ground in trees, and inspected every other day for the appearance of adult males. The first application coincided with the first E. recissoriana catch.

The experiment was executed with a completely randomized design. Four treatments were com-pared: an untreated check, a single application (9 May), a double application (9 May and 13 June), and a triple application (9 May, 13 June, and 18 July). Each insecticide treatment was randomly assigned to 12 trees; 22 trees were randomly assigned to the untreated check. We selected trees spaced sufficiently apart to avoid con-tamination. As a result, we occasionally replaced randomly selected trees if they were too tall or too close to adjacent trees.

Before the first insecticide application, all cones on the treatment and check trees were examined and counted. Before each subsequent insecticide application, all cones were re-examined for obvious insect damage or the presence of L. occidentalis adults or nymphs. Cones with insect damage or insects present were flagged, numbered, and left on the tree. A final observa-tion was made on 21 and 22 August. Previously infested and newly infested cones were collected and bagged separately and returned to the labora-tory in Berkeley, California. The remaining cones were picked from 22 to 25 August. Cones were counted, put in separate burlap bags, and air dried.

The seed was extracted at the USDA Forest Service Coeur d'Alene Nursery, Idaho. Uncleaned seed lots from each tree were put in plastic bags and mailed to Berkeley. All seed lots were carefully clean-ed. Eight groups of 100 seeds from each tree were weighed and placed in envelopes. The remaining seeds were also weighed. Seeds per tree were estimated based on the mean weight of the 800 seeds for that tree. In lots with less than 800 seeds, all seeds were counted.

The eight envelopes with 100 seeds per envelope were taped to an 8 by 10 inch (20 by 25 cm) sheet of paper and radiographed to determine percentages of empty seed, seed with a viable embryo, or seed damaged by L. occidentalis or some unknown cause. Individually collected cones damaged by insects were air dried and the seed were extracted by shaking. Seeds from each cone were counted and radiographed. Data from infested and noninfested cones were combined and used to calculate cone and seed yields for each tree.

The response variables were number of cones harvested per tree, proportion of cones infested, and number of seed per cone. Analysis of variance and analysis of covariance with the number of cones per tree as the covariate were used to detect differences between treatments at the $\alpha = 0.05$ level. Bonferroni's t-statistic (Miller 1980) was used to compare means and to maintain a $\alpha = 0.05$ for all comparisons (Jones 1984). Percentages of filled, empty, or damaged seed were also computed.

RESULTS AND DISCUSSION

Sandpoint-Conophthorus

Beetles began to emerge on 18 April, 1981, and trees were first sprayed on 19 and 20 April. Trees were resprayed on 2 May. No statistically significant difference occurred in the mean number of cones per tree by treatment (table 1). All permethrin treatments had levels of infested cones that were significantly different from the untreated controls. Additional pairwise comparisons revealed the following statistically significant relationships in percent loss of cones: 0.03 pct. once < 0.06 pct. once < 0.12 pct. once = 0.03 pct. twice < 0.06 pct. twice < 0.12 pct. twice (table 1). Percent loss of cones ranged from 75.8 pct. in the untreated controls to 1.7 pct. in the 0.12 pct. double treatment (table 1).

Moscow-Dioryctria

No statistically significant differences occurred between treatments in the number of cones harvested per tree (table 2). However, the final number of cones varied considerably between trees, and ranged from 11 to 186. Dioryctria abietivorella infested 46.6 pct. of the cones in the untreated check. This was significantly more than in any of the insecticide treatments. The proportion of infested cones among insecticide treatments did not differ significantly (table 2). Furthermore, we found no statistically significant relationship between the number of cones on a tree and the proportion of the cones which were infested.

Observations in the seed orchard in previous years indicated the presence of three potential pests of cones and seeds. Although E. recissoriana was present and captured in pheromone traps during 1984, we saw little evidence of damage by this species. Leptoglossus occidentalis also had been abundant during past years, but very few insects were observed during our test. Little, if any, cone damage was observed until 16 July 1984 (fig. 1). All damage was apparently caused by D. abietivorella. In July, less than 4.0 pct. of the cones receiving the single application of 0.025 pct. fenvalerate were damaged by coneworms, whereas ca. 25 pct. of the untreated cones were infested. By August, the proportion of damaged cones on untreated trees increased to 46.6 pct. while only 13.6 pct. of the cones on trees sprayed once and 4.1 and 5.1 pct. of the cones on trees receiving two and three sprays, respectively, were damaged (fig. 1; table 2).

Double or triple applications of 0.025 pct. fenvalerate increased seed yield significantly compared to the untreated check, that is, from 31.3 to 56.0 or 50.0 seeds/cone. The 95 pct. confidence interval for the difference in mean seeds/cone between two applications of fenvalerate and the untreated check is 24.7±15.3. In other words, we are 95 pct. confident that this treatment increased seed production by at least 9.4 seeds/cone (an increase of 30.0 pct.), and possibly as much as 40.0 seeds/cone (an increase of 127.8 pct.).

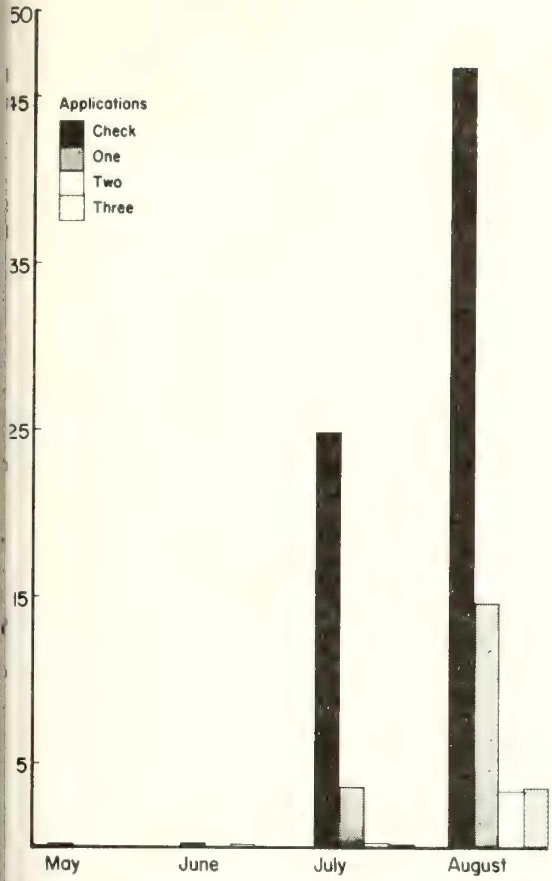
Analysis of covariance showed no effect of cone crop size on number of seed per cone during 1984. All treatments also had approximately the same proportion of filled, empty, and damaged seed (table 2). This undoubtedly results from little or no feeding by L. occidentalis and random oviposition behavior of D. abietivorella.

The high cost of establishing seed orchards and the fact that these orchards are the primary, if not sole, source of resistant western white pine seed make the develoment of effective insecticide treatments an important research effort. The

Table 1.--Infested and noninfested western white pine cones, by permethrin treatment

Treatment	Cones infested	Cones noninfested	Mean cones/tree[1]	% loss of cones[1]
0.03% once	254	234	48.8a	52.0b
0.06% once	203	379	58.2a	34.8c
0.12% once	105	353	45.8a	22.9d
0.03% twice	131	478	60.9a	21.5d
0.06% twice	66	600	66.6a	9.9e
0.12% twice	8	488	45.6a	1.7f
Untreated	547	174	72.1a	75.8a

[1]Means in a column followed by the same letter are not significantly different at the $\alpha = 0.01$ level.



igure 1.--Percent of western white pine cones amaged by Dioryctria abietivorella. Single pplications of 0.025% fenvalerate were applied on May, 13 June and 18 July.

ountain pine cone beetle C. ponderosae was the nly insect of concern in the Sandpoint Seed rchard in 1981. This insect has destroyed up to 5 pct. of the cone crop in this seed orchard. A ingle 0.03 pct. application of permethrin signi-ficantly reduced losses of the cone crop when ompared to the untreated check (from 75.8 pct. oss to 52.0 pct. loss). Two applications of 0.12 pct. permethrin nearly eliminated cone losses. However, 0.06 pct. permethrin applied once was the most cost effective (Shea and others 1984). The fir coneworm D. abietivorella was the only insect species to cause noticeable damage in the Moscow Seed Orchard in 1984. This insect damaged almost half the cone crop on unprotected trees and reduced seed yield by about 44 pct. Two applications of 0.025 pct. fenvalerate, once in May and once in June, significantly increased seed yield. A single application in mid-June might have been sufficient to prevent coneworm damage, but was not tested. A third application in July was apparently unnecessary.

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able 2.--Cones harvested per tree, percentage of coneworm-infested[1] cones, and seed per cone for trees eated once, twice, or three times with 0.025% fenvalerate

eatments[2]	Cones/tree[3]	Infested Cones[3]	Seed/cone[3]	Filled seed[3]	Empty seed[3]	Damaged seed[3]
		Percent		Percent	Percent	Percent
ice	59.8 (8.8)a	13.6 (9.7)b	43.4 (9.0)ab	82.4a	17.1a	0.5a
ice	62.1 (8.8)a	4.1 (9.7)b	56.0 (9.0)b	84.9a	14.8a	0.3a
ree times	65.8 (8.8)a	5.1 (9.7)b	50.0 (9.0)b	85.5a	13.8a	0.7a
eck	56.8 (6.5)a	46.6 (6.7)a	31.3 (6.6)a	85.9a	13.5a	0.6a

nfested by Dioryctria abietivorella (Groté).

wenty-two trees were untreated and 12 trees each received either one, two, or three applications of nvalerate.

ean (±95% confidence limit). Means in a column followed by the same letter are not significantly different Bonferroni's t-statistic at the α = 0.05 level (Miller 1980).

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INSECT PROBLEMS AND CONTROL EFFORTS ASSOCIATED WITH SELECTED DOUGLAS-FIR PLUS TREES

William F. Johns

ABSTRACT: The Beaverhead National Forest has ground-sprayed and implanted their Douglas-fir (Pseudotsuga menziesii) plus trees in an effort to overcome effects of the western spruce budworm (Choristoneura occidentalis) on cone crops. Both methods were successful in protecting cones, but implants have several advantages over spraying.

INTRODUCTION

The tree improvement program for Douglas-fir (Pseudotsuga menziesii) calls for cones to be collected from each of the plus tree stands assigned to the Beaverhead National Forest. The seedlings from these cones will be grown in a progeny test plantation. This stage of the tree improvement program has been held up for several years due to the absence of cones in our Douglas-fir. Even without the effects of insects, good cone crops in Douglas-fir are infrequent on the Beaverhead National Forest.

Added to the natural phenology of the plant is the fact that Douglas-fir on the Forest has been heavily infested with the western spruce budworm (Choristoneura occidentalis) for a number of years. The effect of the budworm on Douglas-fir cone production is twofold: first, the budworm feeds on new foliage, lowering the tree's vigor and thereby lowering the tree's ability to produce cones. Second, the larvae feed on conelets causing cone mortality.

CONTROL EFFORTS

Around January 9, 1982, bud conditions indicated that 1982 would be a good cone year. Shortly thereafter, I contacted Jed Dewey, Regional Entomologist, Forest Service Northern Region, about what the Forest could do to overcome the negative effects of the budworm on cone production. With the help of Jed and Larry Stipe, a program was established to ground-spray our individual plus trees with a mixture of carbaryl and water.

Between June 24 and July 15, 33 stands were sprayed. The upper limit of the spray machine was about 50 feet. At the time I felt that upward drift would give us protection on to the top of the tree. I later came to feel that this was not the case. We did feel that the spray program was successful in that it allowed us to collect cones from many of our stands.

In 1984 we decided to try Acecap implants. In retrospect, that was probably a poor decision due to the poor cone crop. We had not done our homework on cone crop forecasting and were able to collect from only five of the 25 stands that were implanted. Neither method controlled cone midges.

PROJECT COSTS

Very poor cost records were kept on the spray project, but it took about 20 person-days to spray 33 stands. It took more time than desirable because our stands are scattered and I was unfamiliar with their locations.

Accurate cost records were kept on the implant operation. Fifty trees in 25 stands were implanted at a cost of \$2,485. At \$50 per tree, the cost seems to be excessive, but we had already collected from easy-to-reach stands with the spray operation. The biggest factor that drove up the costs was snowmobiling into the stands.

SUMMARY

To summarize, I feel that both operations were worthwhile, but the implants have considerable advantages over spraying. They are:

1. Access with a vehicle is not critical.
2. Height of the tree is not a factor.
3. Weather is not a factor.
4. Individuals do not come in contact with the chemical.
5. There is virtually no chance of environmental contamination.
6. Coverage is more consistent.

Probably the weakest part of our program during this time has been the ability to make an early estimate of our upcoming cone crop. The knowledge exists to make such an estimate; we just need to concentrate more on getting it done. In spite of our poor performance in cone forecasting, however, the use of chemicals has allowed us to reach a point where our collections are almost completed.

This spring indications were that a fair cone crop was coming so we implanted our remaining uncollected stands (18).

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IMPLANTATION AND INJECTION OF SYSTEMICS TO INCREASE SEED YIELD IN DOUGLAS-FIR

Richard C. Reardon and Larry E. Stipe

ABSTRACT: The western spruce budworm, Choristoneura occidentalis Freeman, and spruce coneworm, Dioryctria reniculelloides Mutuura and Munroe, cause widespread damage to cones of Douglas-fir, Pseudotsuga menziesii var. glauca (Beissn.) Franco. The systemic insecticide acephate injected at 4-inch (10-cm) and 6-inch (15-cm) spacings, and implanted at 4-inch spacing in Douglas-fir, increased the yield of filled seeds when compared to the checks.

INTRODUCTION

Douglas-fir, Pseudotsuga menziesii var. glauca (Beissn.) Franco, seed production areas as well as natural stands are subject to unpredictable year-to-year variation in cone crops. In the northern Rocky Mountains, western spruce budworm, Choristoneura occidentalis Freeman, is often the most serious insect pest affecting Douglas-fir cones (Dewey 1970). Other major insect pests are the Douglas-fir cone moth, Barbara colfaxiana (Kearfott); the Douglas-fir scale midge, Contarinia washingtonensis Johnson; the Douglas-fir seed chalcid, Megastigmus spermotrophus Wachtl (Dewey 1968, 1969); and the spruce coneworm, Dioryctria reniculelloides Mutuura and Munroe.

Historically, attempts to suppress populations of seed and cone insects have relied on chemical insecticides applied as foliar sprays (Dewey and others 1975; Stipe and Hard 1980; Stipe and Green 1981). This strategy is not practical for widely scattered trees in rough terrain or where adjacent areas might be sensitive to contamination. Implantation and injection of systemic chemical insecticides offer promise for individual tree protection.

Medicaps are the most widely used implantation method. Medicaps containing powdered acephate and designated as ACECAPS[R] have been used to protect foliage and reduce western spruce budworm larval populations on Douglas-fir and grand fir, Abies grandis (Dougl.) (Markin 1979; Reardon and Haskett 1981; Reardon 1984a; Reardon and Barrett 1984). ACECAPS[R] implanted at 4-inch (10-cm) spacing are registered for control of spruce budworms in the United States (Reardon 1984b).

Mauget systemic injector units containing oxydemeton-methyl and designated Inject-A-Cide[R] are effective in reducing insect populations and increasing seed yield on Douglas-fir in California (Koerber 1978; Dale and Frank 1981). At present, mauget units with acephate are not registered for control of spruce budworms.

This paper reports a study to determine the effectiveness of Medicaps containing acephate or dimethoate and Mauget systemic injector units containing oxydemeton-methyl or acephate at two spacings in increasing the seed yield of Douglas-fir. Nutrients were also injected at 6-inch (15-cm) spacing.

MATERIALS AND METHODS

The study area of 500 acres (200 ha), about 10 mil (16 km) west of Whitehall, MT, contained open-grow Douglas-fir at ca. 5906 feet (1800 m) elevation. The trees ranged in height from 33 feet (10 m) to 64 feet (20 m) and averaged 37.1 ± 2.3 cm ($\bar{x}$ ± SD) in diameter at 4 inches (10 cm) from the soil surface. Most of the sample trees were separated by a distance of at least 20 m, numbered and randomly assigned one of eight treatments: oxydemeton-methyl injected at 10- or 15-cm intervals, nutrients injected at 15 cm, acephate injected at 10 or 15-cm, dimethoate or acephate implanted at 10 cm, and untreated checks. There were 20 sample trees per treatment except for acephate injected at the 10-(8 trees) and 15-cm (10 trees) spacings, due to a limited number of injector units.

Trees were treated on 6 and 7 April 1982, when cone buds were swollen and vegetative buds were still tight.

The powdered formulations of acephate (97 percent Orthene) and dimethoate (95 percent Dimethoate) we introduced directly into the xylem by using Medicap plastic cartridges (1 cm x 3 cm). Each acephate cartridge contained 0.9 gm active ingredient (AI) and each dimethoate cartridge contained 0.6 gm AI.

Liquid formulations of oxydemeton-methyl, as 50 percent Metasystox-R[R]; acephate, as 35 percent Orthene; and nutrients, as 1 percent iron and 1 percent zinc, were injected into the xylem by using Mauget injection units. Each unit contained 1.5 g AI of oxydemeton-methyl or 1.8 g AI of acephate. The Mauget injectors were removed after 12 days.

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'our methods were used to process mature cones-- ιir drying and shaking in bags, axial slicing, lismantling, and nursery processing; thereby, :our estimates of the proportion of filled seeds ›er cone were obtained per treatment. Fifty ıature cones were collected from the upper half ›f the crown from each sample tree on 30 August .982. Twenty-five of these cones were placed in ι paper bag, allowed to air dry, shaken, and the ›roportion of opened cones, external cone lamage, and total dislodged seeds per tree were 'ecorded. One hundred seeds from each tree were 'andomly selected and X-rayed to determine the ›roportions that were filled, hollow, and damaged ›y insects.

'he other 25 cones from each tree were bisected .ongitudinally along the cone axis with cone :utters. One cut surface of each cone was :xamined for the number of seeds filled, hollow, ınd damaged by insects (Dobbs and others 1976). ι subsample of 10 sliced cones per tree was lismantled by removing one scale at a time from :he axis. The average number of seeds damaged by .epidopterous larvae, and numbers of scale midge ınd Douglas-fir cone-gall midge, Contarinia ›regonensis Foote, per cone were recorded.

'hree 1-bushel (35.2-L) samples of mature cones 'ere collected per treatment on 1-3 September .982, with pole pruners and by climbing the trees. :ach 1 bushel of cones was collected from at .east three sample trees for a treatment. At .uck Peak Nursery in Boise, Idaho, the cones were ιir and kiln dried, followed by tumble extraction ›f the seeds, seed dewinging, and air separation ›f filled and hollow seeds. A subsample of 300 :eeds taken from the seeds determined as "filled" by air separation that were recovered from each bushel were X-rayed to determine the proportion filled, hollow, and damaged by insects. A subsample of 200 sound seeds recovered from each bushel was forwarded to the Idaho State Seed Laboratory to assess germination.

All data were analyzed by using the Games and Howell T modification for paired multiple comparisons with unequal variances (Keselman and Rogan 1978).

RESULTS

Damage by insects, as measured for mature cones processed by shaking, by axial slicing, and by dismantling, was significantly less in some treatments (table 1). The average proportion of external cone damage for each treatment, except nutrients and dimethoate, was significantly less than that for the checks. The average proportion of opened cones for each treatment provided an additional estimate of external cone damage; significant differences between treatments and checks were similar to those for external cone damage.

For the mature cones bisected longitudinally, the average insect-damaged seed per cone surface was significantly less for acephate injected at 10-cm intervals than that for each of the other treatments and checks.

For mature cones that were dismantled, the average number of seeds per cone damaged by lepidopterous larvae was significantly less for each acephate treatment than for the checks.

Table 1.--Insect damage to Douglas-fir cones on trees injected or implanted with systemic insecticides or nutrients, Montana 1982

Treatment	Shaking			Slicing		Dismantling			
	Cones processed per treatment	External cone damage (%)[1]	Cones opened (%)[1]	Cones processed per treatment	Insect-damaged seeds per cone surface[1]	Cones processed per treatment	Insect-damaged seeds per cone[1]		
							C. oregonensis	C. washingtonensis	Lepidopteran
		$\bar{X} \pm SE$	$\bar{X} \pm SE$		$\bar{X} \pm SE$		$\bar{X} + SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$
Injected									
Oxydemeton-methyl									
15 cm	500	29.7[1] ± 3.1 b	63 ± 1.0 b	494	1.8 ± 0.4 a	200	0.44 ± 0.16	0.07 ± 0.04	9.9 ± 1.2 a
10 cm	475	33.2 ± 2.9 b	54 ± 1.1 b	475	3.0 ± 0.4 a	200	0 -	0.42 ± 0.18	9.5 ± 1.4 a
Acephate									
15 cm	250	17.9 ± 4.2 b	76 ± 1.4 c	250	1.8 ± 0.3 a	100	0 -	0.65 ± 0.31	8.5 ± 1.3 b
10 cm	160	10.0 ± 3.5 c	88 ± 0.0 c	198	0.7 ± 0.2 b	80	0.90 ± 0.38	0.11 ± 0.10	3.1 ± 0.6 b
Nutrients--15 cm	500	43.2 ± 3.4 a	40 ± 1.1 a	492	2.1 ± 0.3 a	200	0.67 ± 0.23	0 -	13.3 ± 1.4 a
Implanted									
Acephate--10 cm	500	20.7 ± 3.6 b	64 ± 1.3 b	498	1.9 ± 0.3 a	200	0.15 ± 0.01	0.29 ± 0.11	4.5 ± 1.0 b
Dimethoate--10 cm	450	41.5 ± 4.1 a	48 ± 1.4 a	488	2.5 ± 0.3 a	200	0.06 ± 0.04	0 -	10.5 ± 1.1 a
Checks	500	50.7 ± 3.9 a	43 ± 11.3 a	493	3.0 ± 0.4 a	200	0.16 ± 0.08	0 -	14.6 ± 1.2 a

[1]Means in the same column followed by the same letter do not differ significantly (P>0.05).

Most damage to seeds and cones was caused by the western spruce budworm and spruce coneworm. Insects found in low numbers (avg. < 1 per cone) were the Douglas-fir seed chalcid, cone-scale midge and cone-gall midge.

Trees treated with dimethoate or nutrients consistently yielded greater numbers of filled seeds per cone than did the checks, but the difference was not significant (table 2). Significantly and consistently greater numbers of filled seeds per cone were detected, except for the nursery process, for oxydemeton-methyl at 15-cm intervals, and for acephate implanted and injected at 10 and 15-cm intervals, compared with the checks. Oxydemeton-methyl at the 10-cm spacing was not as consistently effective at 15-cm even though more insecticide was injected into each tree.

DISCUSSION

Oxydemeton-methyl at 15-cm intervals, acephate injected at 10- and 15-cm intervals and implanted acephate consistently and significantly increased the number of filled seeds per cone when compared with the checks. Acephate injected at 10-cm intervals was more effective than the oxydemeton-methyl treatments in protecting cones, as determined by external cone damage and percentage of opened cones, and seeds from damage by lepidopterans.

Air drying and shaking was the least time consuming of the four methods used to process mature cones. Numbers of filled seed per cone determine by this method were higher than determined by axial slicing, lower than by dismantling, and higher than by processing at the nursery.

Medicaps, with implanted acephate at 10-cm intervals and Maugets, with injected acephate at 10-cm intervals, are both effective in reducing larval densities of western spruce budworm and spruce coneworm and in increasing the number of filled seed per cone for Douglas-fir. Medicaps are registered for use against spruce budworms an do not require removal of the empty cartridge fro the drilled hole. Maugets, with acephate, are no registered for use against spruce budworms, although the company has petitioned for registration. Both Medicaps and Maugets containing acephate are available at the same cost per cartridge or unit.

Table 2.--Filled Douglas-fir seed per cone (means ± SE) by treatments and cone-processing methods, Montana, 1982

Treatment	Shaking	Slicing (per cone surface)	Dismantling	Nursery Processing
Injected				
Oxydemeton-methyl				
15 cm	13.8 [1/] ± 1.6 b	4.1 ± 0.5 b	15.3 ± 2.0 b	6.6 ± 1.C
10 cm	9.4 ± 1.1 a	3.2 ± 0.4 b	12.0 ± 1.3 b	7.6 ± 1.6
Acephate				
15 cm	13.6 ± 1.3 b	4.3 ± 0.7 b	11.0 ± 1.2 b	9.5 ± 1.6
10 cm	16.0 ± 2.6 b	3.3 ± 0.4 b	17.6 ± 2.9 b	8.4 ± 0.8
Nutrients--15 cm	8.0 ± 1.2 a	2.3 ± 0.3 a	9.5 ± 1.3 a	8.5 ± 0.8
Implanted				
Acephate--10 cm	14.9 ± 1.9 b	5.0 ± 0.5 b	16.9 ± 1.6 b	13.9 ± 2.9
Dimethoate--10 cm	7.0 ± 1.3 a	2.8 ± 0.4 a	10.3 ± 1.5 a	5.7 ± 1.0
Checks	5.5 ± 0.9 a	1.6 ± 0.2 a	6.0 ± 0.7 a	5.6 ± 0.7

1/ Means in the same column followed by the same letter do not differ significantly (P > 0.05).

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IMPACT OF INSECTS ON CONE/SEED PRODUCTION IN THREE

BLISTER RUST-RESISTANT WESTERN WHITE PINE SEED ORCHARDS

Patrick J. Shea

ABSTRACT: Little is known about the impact of insects on production of blister rust-resistant western white pine seed. Results from sampling the only three producing seed orchards in Idaho indicate insects can severely reduce production. Further, the insect species responsible for damage differ among the various orchards. A recommendation for locating future orchards in white pine type is made based on the potential for minimizing insect-caused seed losses.

INTRODUCTION

A significant accomplishment of the breeding program for blister rust-resistant western white pine (BRR/WWP) is the establishment of three producing seed orchards in Sandpoint, Coeur d'Alene and Moscow, Idaho (Bingham 1983). Western white pine, _Pinus monticola_ Douglas, is valued for its clean-boled form, and soft, white, easily-processed lumber. It regenerates naturally and is characterized by relatively rapid initial and continued growth. The effect and history of the introduced fungus, _Cronartium ribicola_ Fisher, on WPP, and attempts by federal and state agencies to combat the spread of blister rust is well known (Haig and others 1941; Hepting 1971). Because of its economic importance, forest land managers of the northern Rocky Mountains have made the reestablishment of WWP to its former habitat a priority management objective.

Specific data are lacking on the effects of insects on production of BRR/WWP seed. However, insects are suspected of being responsible for substantial seed losses in all three orchards. Previous research in the Sandpoint orchard strongly indicates that _Conophthorus ponderosae_ (=_C. monticola_ Hopkins), the mountain pine cone beetle, is the insect primarily responsible for losses of up to 90 percent of the cones (Jenkins 1982; Bingham 1983). The situation in Moscow and Coeur d'Alene is not quite as clear. Observations by Forest Pest Management, R-1, and orchard personnel indicate that at least three insect genera are present and probably cause substantial loses. Species such as _Leptoglossus occidentalis_ (Heidemann), western conifer seed bug, _Eucosma recissoriana_ Heinrich, lodgepole pine cone borer, and one or more species of _Dioryctria_, the fir coneworms have been reared from cones. If we are to develop pest management systems for these orchards, it is critical that we accurately assess the impact of insects on BRR/WWP seed, and attempt to rank or quantify the amount of seed damaged by each insect species. The objective of this paper is to present the results of the 1984 sampling efforts.

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MATERIAL AND METHODS

The three producing orchards were periodically sampled for insect damage throughout the late spring and summer of 1984. The northernmost orchard is located in Sandpoint, Idaho. It was established in 1960, and is about 17 acres (7 ha) in size. It contains 800 grafts from 13 clones and has been producing harvestable quantities of cones since 1978. In this orchard 24 trees, ranging from 20-45 ft (9 to 15 m) in height, were randomly selected for study.

The Coeur d'Alene orchard is located approximately 42 miles (67.5 km) south of Sandpoint. This orchard was established in 1960 and is about 13 acres (5 ha) in size. It is considered a low-elevation orchard and is stocked by the same families that occur in the Moscow Arboretum. This orchard is just beginning to produce harvestable quantities of cones but still requires artificial pollination. It had very few cone bearing trees in 1984 so that it was possible to examine the cones on all trees (68) that had at least three cones per tree.

The Moscow Arboretum is located about 70 miles (112.7 km) south of Coeur D'Alene and beginning in 1957 was planted with WWP seedlings that survived intense, artificial inoculation with blister rust (Hoff and Coffen 1982). This orchard covers about 23 acres (8 ha), and 22 trees 20-45 ft (9-15 m) in height were randomly selected for study. The seed produced by this orchard is shared among the 11 cooperatives in the Inland Empire Cooperative Tree Improvement Program. Only trees in the NW quadrant of the orchard were used. It is noted that this orchard is on the edge of the Palouse and is quite some distance (> 50 miles [129 km]) from any natural stands of WWP.

A hydraulic manlift was used to sample all trees. The first sample (May 18, 1984) was started one week after the second-year cones began to elongate. All cones on all sample trees were examined for insect entrance holes, presence of _L. occidentalis_ (nymph or adult), or any other external evidence of damage. Mean numbers of cones per tree were calculated for all orchards and ANOVA (alpha =.05) was used to detect significant

differences between orchards. Mean numbers of seeds per cone were calculated for the Moscow and Coeur d'Alene orchards only. Damaged cones were flagged and coded so that individual cones could be re-examined throughout the summer. At the end of the summer all damaged cones were removed and taken to the laboratory where they were dissected. The remaining cones on all sample trees in Coeur d'Alene and Moscow were picked, counted, put in separate labeled burlap bags, and air dried. Seeds were extracted at the USDA Forest Service Coeur d'Alene Nursery. These uncleaned seeds were put in plastic bags and shipped to Berkeley, CA for analysis. Seed lots were kept separate by tree. Eight envelopes per tree with 100 seed per envelope were radiographed to determine percentage of filled seed with viable embryo and empty seed, or seed damage by L. occidentalis, or some other unknown cause. This provided the estimate for seeds per cone and damage by L. occidentalis.

RESULTS AND DISCUSSION

In 1984, the Sandpoint Orchard had significantly more cones per tree (88.8 cones per tree) than either Moscow (56.9 cones per tree) or Coeur d'Alene (5.2 cones per tree)(alpha = .05, table 1). The small cone crop in Coeur d'Alene compared to either Moscow or Sandpoint was not unexpected since this orchard has just recently begun to produce cones. However, cone production would have been much higher than 5.2 cones per tree except that there was a high rate of cone abortion in the fall of 1983. The yield of 31.3 seeds per cone in the Moscow Arboretum is not much different than the 39 seeds per cone reported by Hoff and Coffen (1982) for this same orchard. The very low seed per cone (10.2) yield at Coeur D'Alene is thought to be due to poor pollination.

Five species of insects from three orders and four genera cause damage to BRR/WWP seeds and cones in the three orchards. When cone beetles emerge from overwintering diapause, the adult females attack maturing cones and kill them in the process. Each attacking female is later joined by an adult male. After mating she lays eggs as she feeds down the axis of the cone. One female may attack several cones (Jenkins 1982; Williamson and others 1966). Upon hatching, the larvae begin feeding throughout the cone. Both adult and immature forms of the western conifer seed bug feed on the individual maturing seeds of a wide range of conifers. The life history and habits of the seedbug on WWP are not completely known, but in natural Douglas-fir stands, there is one generation per year with ovipositing adults present from May to July and immatures from June to September (Hedlin and others 1980). This generally coincides with our observations in 1984. The fir coneworms and the lodgepole pine cone borer both attack the cones of several species of conifers. Adults oviposit on the surface of developing cones and the resulting larvae mine throughout the cone and destroy much of the seed. Preliminary results of pheromone trapping in 1984 and 1985 indicate that E. recissoriana adults begin to appear in the orchard in early June. In 1985, Dioryctria spp. were not captured in pheromone traps until two weeks after the first E. recissoriana were caught.

The Moscow and Coeur d'Alene orchards experience considerably more cone damage, 46.6 percent and 47.3 percent respectively, than the Sandpoint orchard (10.4 percent) (fig. 1). In Moscow virtually all the damage was attributed to the fir coneworms and perhaps the lodgepole pine cone borer (fig. 2). We have been unable to assess the amount of damage by species in this orchard. Very few seed bugs were observed in the orchard during sampling. In Coeur d'Alene, D. abietivorella was the only lepidopteran species causing damage; 37 percent of the cones were infested with larvae of this species. Cones killed by C. ponderosae were also collected from this orchard but in relatively

Table 1.--Number of trees sampled in each of three western white pine seed orchards, 1984

Orchard	N	Mean Cones/Tree (±SE)	Mean Seeds/Cone (±SE)
Moscow	22	56.9 (±6.1)	31.3 (3.16)
Coeur d'Alene	68	5.2 (±2.2)	10.2 (0.68)
Sandpoint	24	88.8 (±12.1)	NA

NA = Not assessed.

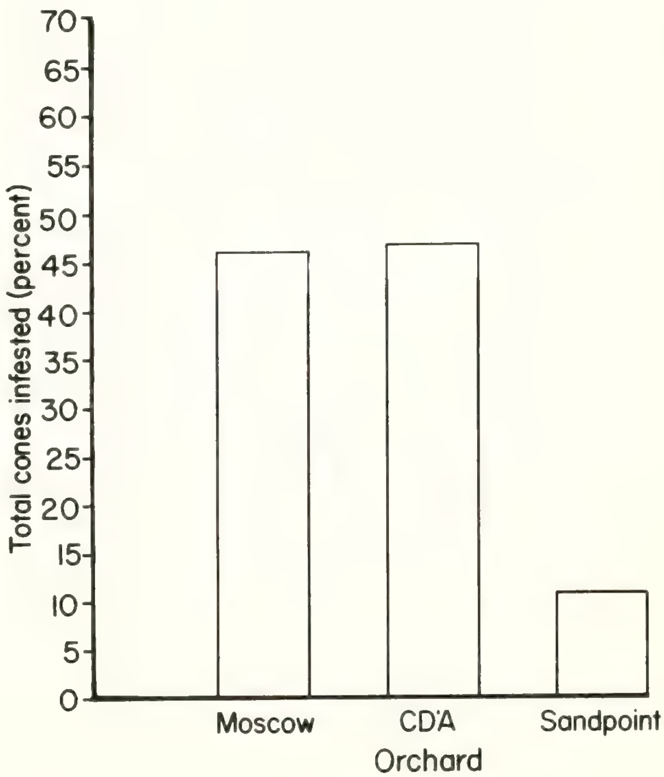

Figure 1.--Total percentage of infested cones in western white pine seed orchards, 1984.

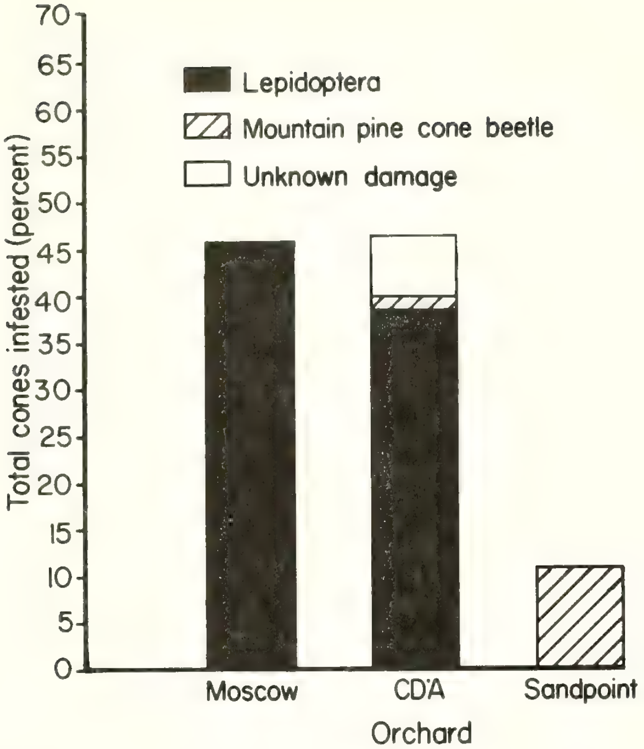

Figure 2.--Percentage of infested cones by insect group for western white pine seed orchards, 1984.

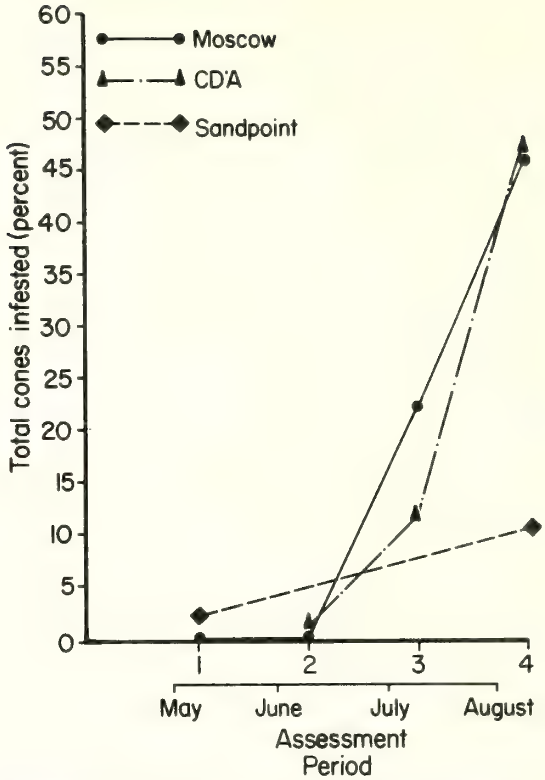

Figure 3.--Percentage of infested cones by sampling date in western white pine seed orchards, 1984.

small numbers (fig. 2). L. occidentalis populations were heaviest at Coeur d'Alene and results of radiographed seed reveal that 12 percent of the seed were destroyed by adults and immatures of this species. The full impact of L. occidentalis on production of BRR/WWP is not fully captured by x-ray analysis of seed. There is considerable suspicion that this insect may be responsible for a large share of the conelet abortion experienced in Coeur d'Alene during the fall of 1983. Studies are in place to validate whether L. occidentalis is causing conelet abortion and, if so, to what extent. C. ponderosae was the only insect species causing damage in the Sandpoint orchard (fig. 2). None of the lepidopteran species were recovered in Sandpoint and only an occassional L. occidentalis was observed.

Earliest damage occurs in the Sandpoint orchard during late April to mid-May, with the emergence of adult female cone beetles (fig. 3), but the attack period is completed by mid-June (Jenkins 1982; Shea and others 1984). At Coeur d'Alene and Moscow, visible damage begins to appear in mid-June and continues to accumulate through August (fig. 3).

Several tentative observations can be made from the 1984 impact study, all of which relate to the development and implementation of an IPM system. First, there appear to be distinct differences in the insect complex associated with the three BRR/WWP seed orchards. Second, there may be an association between the amount of damage experienced and the number of species causing damage. The more pest species in the orchard the greater the damage, e.g. Moscow vs. Sandpoint. Thirdly, in those orchards with multiple pest species the period of cone and seed vulnerability or insect attack period is longer than it is in the orchards with a single pest species such as Moscow vs. Sandpoint. If these initial observations are confirmed during the remaining two years of study, development and implementation of an IPM system in each orchard could be profoundly affected. For instance, decisions regarding management strategies to protect cones from damage in orchards with multiple pests may be quite different than in orchards with a single pest, i.e. multiple insecticide applications vs. a single application; or multiple monitoring systems vs. single monitoring system.

Lastly, note that the Sandpoint orchard is the only one of the three orchards studied that is located in white pine type; whereas, both the Moscow and Coeur d'Alene sites are located out of type. In addition, note that the three lepidopteran species and L. occidentalis can all be considered generalists as defined by Fox and Morrow (1981), that is they utilize a more diverse array of host plants than does C. ponderosae (Hedlin 1981). This suggests that contrary to the recommendation of Hoff and Coffen (1982) and Bingham (1983), it may be advantageous to locate future BRR/WWP seed orchards in white pine type. In doing so the orchard manager may only be concerned with management of a single pest as compared to a multiple pest situation and its attendant complexity.

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INFLUENCE OF DISEASES ON SEED PRODUCTION

Jack R. Sutherland

ABSTRACT: In this, the first of three papers on the influence of diseases on seed production, hosts, life cycles and damage, and management recommendations are given for important diseases of Inland Mountain West seed orchard trees, cones and seeds. Highlighted are Armillaria root rot, needle diseases, Inland spruce cone rust, the seed or cold fungus and Sirococcus blight.

INTRODUCTION

Although foresters and pathologists have always assumed that diseases affect seed production, it is only with the recent development of seed orchards and container nurseries that the importance of diseases of seed-producing trees and their crop have begun to be clearly defined. The high value and feasibility of protecting seed orchard trees and their cones and seeds has both necessitated and justified the development of management strategies for these diseases while container seedling production has demonstrated the importance of seed-borne pathogens in seedling disease incidence and losses. Many seed-borne problems either did not develop, were not evident, or were attributed to other causes in bareroot nurseries. Because of the increasing demand for high quality seeds we need to know how to recognize and manage diseases that affect seed orchard trees, cones and seeds and seedling pathogens such as Fusarium that are seed-borne. Not only have technological advancements increased our awareness of these various diseases, but new techniques such as the use of monoclonal antibodies have changed and improved our methods of assaying for pathogens. My goal and that of Drs. James and Mitchell in this portion of the symposium is to update and synthesize what is known about diseases affecting conifer seed production in the Inland Mountain West.

Review paper presented at the Conifer Tree Seed in the Inland Mountain West Symposium, Missoula, MT. August 5-6, 1985.

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DISEASES OF SEED ORCHARD TREES

Any tree disease likely harms seed production o quality (e.g. Schaffer and others 1983). This is true even when the disease results in increased cone production such as happens with distress cone crops on root-rot diseased trees because probably such cones yield inferior seeds. To date there is no evidence that it is worthwhile controlling diseases of seed producing trees in natural stands, including those where some silvicultural treatment has been used to stimulate or facilitate cone production, thus the following deals only with diseases of seed orchard trees. In seed orchards, tree and crop values plus easy access usually make disease management practical. Potentially, any species of seed orchard tree i susceptible to all the diseases affecting it in nature. However, the special environment of seed orchards created by fertilizing, watering, growing trees out of their natural geographic locality and other practices, may increase the risk and impact of diseases or alter their host range.

Experience indicates diseases encountered on orchard trees varies with the orchard's age. Usually the first to appear are diseases indigenous to the site or those acquired by the seedlings prior to outplanting in the orchard. For example, Armillaria root rot, Armillaria mellea (Vahl.: Fr.) Quel.), has killed 1-2% of the white spruce, Picea glauca (Moench) Voss, i an Interior B.C. orchard in the 5 years following planting, but losses are expected to decrease as inoculum, which was present in the forest that was cleared for the orchard, dies out. Western gall rust, Endocronartium harknessii (J.P. Moore) Y. Hirat., of lodgepole pine, Pinus contorta Dougl. exemplifies a disease that can be brought into a seed orchard on diseased stock. Such seedlings not only introduce the disease into the orchard, but as infection is usually on the bole, the trees are subsequently subject to wind breakage at the infection site or killing of weakened trees by secondary organisms. Presence of indigenous diseases should be one of the major selection criteria in choosing an orchard site. Although presence of a disease usually will not eliminat a potential site, it is best to reduce disease risk as much as possible before orchard establishment. When forest sites are to be use for orchards, survey and mark the root rot centers before clearing the trees, then repeate

root pick the area and especially the disease centers to remove pathogen-infested roots (inoculum). Alternate hosts such as those of lodgepole pine stem rusts (e.g., Indian paintbrush (Castilleja miniata Dougl. ex Hook) should be eliminated from within and adjacent to any proposed pine orchard. Alternate hosts can be prevented from re-invading the site by sowing competing grasses or other cover crops, especially perennials which can withstand repeated mowing which is detrimental to most alternate hosts. Herbicides should be used to kill alternate hosts that re-invade the seed orchard and nearby areas.

As the orchard ages, previously unencountered diseases may appear. These include foliage pathogens which are often favored by the greater volume of needles on larger trees, particularly dead and senescent needles, which may enhance pathogen buildup or survival. Undoubtedly, microclimate within the crown changes as trees become larger and this leads to other changes such as an increased volume of shade and senescent needles. Changes that may favor needle pathogens include higher humidity, longer moisture retention on needles, lower temperatures and decreased exposure to sunlight. At a Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, orchard on Vancouver Island, B.C. Meria laricis Vuill. and a newly discovered fungus, Hormonema merioides Funk, Woods & Hopkinson (Funk and others 1985), both on needles, only became evident in older orchards where cold water misting was used to retard flower development for preventing pollen contamination from outside the orchard. Defoliation was most severe on trees nearest misting stand pipes. As trees reach cone-bearing age the cultural practices change. Crown and sometimes root pruning can cause both wounds (infection courts) and stress. Cone picking can cause wounds too, especially on species such as lodgepole pine. With larger orchard trees there are the increased difficulties of detecting pathogens and applying fungicides.

Little information is available on pathogen-insect associations in Inland Mountain West seed orchards, but recently in coastal B.C. the needle cast fungus Meria has been found in wounds of a needle midge (Contarinia sp.). on Douglas-fir. This resembles a similar situation in loblolly pine, Pinus taeda L., orchards in the southern U.S.A. where the pitch canker Fusarium colonizes needle wounds made by Contarinia (Dwinell and others 1981). Pine wood nematode, Bursaphelenchus xylophilus (Steiner & Buhrer) Nickle, which is both beetle transmitted and host stress related, could occur in orchards as the result of cultural practices such as root pruning (Dwinell and Barrows-Broaddus 1983).

CONE DISEASES

Inland Spruce Cone Rust

This rust, Chrysomyxa pirolata Wint., is the most damaging cone disease in the Inland Mountain West. Cone losses of up to 60% and 67% have been recorded for natural stands in western Canada (Ziller 1974) and Utah (Nelson and Krebill 1982), respectively. Seed orchard cones appear to be equally affected as evidenced by annual losses of up to 60% in the first few years of cone production in an interior B.C. spruce orchard. Cones of all indigenous spruces are susceptible. The alternate (non-conifer) hosts are Pyrola spp. and Monesis uniflora (L.)A. Gray which are relatively small, herbaceous to woody plants. Pyrola spp. are the predominant component of the ground cover in some spruce forests. Although the fungus is holartic in distribution and occurs on alternate hosts as far south as Guatemala (Cummings 1943), cones are only affected in the northern part of its range. Nelson and Krebill (1982) give some of the possible reasons for this. In the Inland Mountain West this disease is likely to be more of a problem in the north than in the south.

The states and spores (in parentheses) in the life history of C. pirolata are spermagonial (spermatia), aecial (aeciospores), uredinial (urediniospores) and telial (teliospores). The first two occur on spruce cone scales; spermatia as a yellow-orange honeydew-type exudate in early summer and as soon as 2 weeks later, dry, yellow-orange aeciospores. Aeciospores are produced in profusion and shed from diseased cones which desiccate and open prematurely. Both the uredinial and telial states occur as yellow-orange sori on the under surface of alternate host leaves. Urediniospores spread the fungus to other alternate host plants and occur, depending upon the species of alternate host and perhaps locality, from late spring through to snowfall, but they are usually most abundant about the time of spruce cone pollination. At this time too, telia, similar in appearance to uredinia, form on the undersurface of alternate host leaves. A leaf may bear mostly uredinia, mostly telia, or both in about equal numbers. Telia produce teliospores which germinate , giving rise to basidiospores which lead to cone infection about pollination time. Information on these various states was recently published (Sutherland and others 1984).

Chrysomyxa pirolata usually becomes systemic in cones which dry out, initially becoming brownish green and later tan-brown, and open prematurely. Resinosis often accompanies these symptoms as does twisting and malformation of cone scales. Sometimes cone rust appears to be restricted to one side of the cone causing it to be slightly convex. Diseased cones should not be collected because they yield few seeds which may germinate poorly or abnormally (Nelson and Krebill 1982; Sutherland 1981A).

Cone rust loss estimates have traditionally been made by counting diseased, aeciospore-bearing cones at collection time; however, such counts underestimate cone rust losses because about one-third of the cones with spermatia in early

summer do not produce aeciospores (Sutherland and others 1984). Instead, shortly after spermatia production the cones cease development, dry out, and are often attacked by insects. In orchards where cones are readily accessible, cone rust appraisals should include comparative counts of spermatia-bearing versus aeciospore-bearing cones. Under forest conditions cone rust severity tends to be sporadic and localized. The disease depends on numerous factors including presence and phenology of the cone crop and disease on alternate hosts, weather conducive to basidiospore production, dissemination and cone infection plus synchronization of these climatic and biological phenomena. As cultural practices such as root pruning induce more regular cone crops, cone rust losses in seed orchards could exceed those in forests. Effects of other seed orchard practices are unknown, e.g., cold water misting to retard cone development might favor the disease in certain years by synchronizing cone and rust phenology. Conversely, misting could reduce losses by preventing spores from reaching susceptible cones.

Prevention of cone rust is easy, provided a seed orchard site is selected that is free of alternate hosts. The B.C. situation demonstrates this with a spruce seed orchard near Salmon Arm, where Pyrolas are abundant, regularly experiencing 15-60% cone losses while spruce orchards about 50 km south in a drier, Pyrola-free, area are free of cone rust. Although it is not known how far viable cone rust basidiospores are carried, it is suspected that disease intensity is directly proportional to closeness of the non-conifer host. Thus, practices that reduce the abundance of alternate hosts immediately around the orchard should be helpful. For example, when sufficient ground fuel was available at Salmon Arm, summer burning eliminated the Pyrolas. Summer application of paraquat or mineral oil (agricultural weed killer) was also effective against Pyrolas. Nitrogen fertilizers (NH_4SO_4 or urea) applied at forest fertilization rates in the spring and fall had no detrimental effects on P. asarifolia Michx. or P. (Orthillia) secunda L. in the second growth forest surrounding the seed orchard. Two years after fertilizer application, neither Pyrola numbers nor the ratio of healthy to diseased plants were changed, but growth of grasses and other understory plants increased dramatically. This suggested that fertilizers might be used to increase understory fuel for burning to eliminate Pyrolas. One area adjacent to the Salmon Arm orchard is pastured, but cattle avoid the abundant P. asarifolia.

Ferbam fungicide, applied to cones during the period beginning 1 week before through pollination, reduces cone rust incidence 7-10 fold (Summers and others 1985). Two sprays are recommended to compensate for differences in cone phenology. Since germination of seeds from treated cones is reduced slightly, an extremely important consideration for container nurseries, other fungicides need testing, especially systemics such as triademefon.

Other Potential Cone Diseases

Examples of other rusts that could damage cones locally include western gall rust (Byler and Platt 1972) of hard pines, spruce bud rust (McBeth 1984), and American spruce-raspberry rust (Ziller 1974). Since these pathogens are not confined to cones the potential damage is very unpredictable, especially to seed orchard cones.

SEED DISEASES

Seed or Cold Fungus

This fungus, Caloscypha fulgens (Pers.) Boud., imperfect state = Geniculodendron pyriforme Salt (Paden and others 1978) is the best known conifer seed pathogen in this area, having been isolated from seeds from Oregon and Washington (Harvey 1980), Idaho (Wicklow-Howard and Skujins 1980) and British Columbia (Sutherland 1979; Sutherland and Woods 1978). Seeds of numerous conifers are susceptible (Salt 1970; Salt and Brown 1969). The fungus occurs naturally on seeds of species with non-serotinous cones that are collected from the ground (Sutherland and Woods 1978), especially from squirrel caches (Sutherland 1979). About one-third of all spruce (Picea spp.) seedlots in B.C. are infested (Sutherland 1979). Other common hosts are seeds of Douglas-fir and true firs, Abies spp., the latter mainly because mature cones disintegrate and the pieces are collected from the forest floor. Seedlots of species such as lodgepole pine that usually have serotinous cones are disease free. Within most infested seedlots 1-5% of the seeds are diseased; however, seedlots with up to 60% affected seeds have been found. Even low numbers of diseased seeds are important because the pathogen spreads from diseased to healthy seeds at low temperatures (Epners 1964), the origin of the cold fungus name (Salt 1974), such as during seed stratification, pre-sowing storage or after sowing in cool, wet seedbeds or container cavities (Thomson and others 1983).

There are both qualitative and quantitative indicators of seed fungus infestation. Seedlots with much poorer germination when stratified are prime suspects. Losses increase as exposure to cool, wet conditions lengthens (Salt 1974). The rate of germination is important since only ungerminated seeds are susceptible, i.e., seeds are immune once germination begins (Epners 1964; Salt 1974). Seeds affected by C. fulgens are mumified and not rotted as are seeds killed by pre-emergence, damping-off fungi (Epners 1964). The seed fungus may also produce patches of indigo pigment in or around the embryo (Salt 1974; Woods and others 1982). White to whitish blue infection cushions of C. fulgens, often most abundant at the seed's distal end, may cover up to 80% of the seed coat surface (Woods

and others 1982). Quantitative determinations can be made by isolating C. fulgens from a 500-seed sample of surface sterilized (30% H_2O_2 for 30 min) seeds which are incubated at 15°C on 2% water agar (Sutherland and others 1978). The distinctive mycelium (Salt 1974), often indigo, grows from seeds within 3 weeks. Another technique (Sutherland and others 1981B) that provides either qualitative or quantitative assays for C. fulgens is based on the presence and amounts of alkaline phosphatase in infested seedlots. A major advantage of isozyme assays is that they allow use of much larger sample sizes than are physically possible with isolation-by-plating procedures.

As stated earlier, seeds acquire C. fulgens when cones contact infested forest duff. Hence, disease incidence increases with exposure time (Sutherland 1981B) and can increase further if contaminated cones are improperly stored, e.g., under cool, wet, poorly ventilated conditions. However, spread ceases if stored cones are properly air-dried (Sutherland 1981B). Seedlots originating from squirrel-cache collected cones are most likely to contain C. fulgens (Sutherland 1979). Squirrels disseminate infested cones and along with other rodents consume diseased seeds (Sullivan and others 1984). Other than disseminating the fungus, conidiospores and ascospores apparently play no obligatory role in disease development because the pathogen penetrates seeds following infection cushion formation by vegetative mycelium (Woods and others 1982). Ascospores are produced in cup-shaped fruit bodies, with a dull to bright orange hymenial layer, which occur on forest duff in early spring (Ginns 1975), often soon after snow melt.

High incidence of C. fulgens is an excellent indicator of improper cone collection or storage, or frequently both. For example, (i) cones were collected that had been on the ground for a long time, (ii) collections were from squirrel caches, and (iii) such cones were improperly stored (cool, wet, poor ventilation). The worst possible situation results from a combination of all three. When collecting cones from natural stands, hand picking them from standing trees or from slash plus proper handling afterward should greatly reduce seed fungus incidence. Since seed orchard cones are usually hand picked and properly handled afterward, the pathogen should not occur in these seeds. Cultural practices that will reduce losses when sowing infested seedlots include: (i) not stratifying the seeds or stratify them for the shortest possible period, (ii) sowing seeds quickly after stratification to avoid pre-sowing storage where the pathogen spreads, (iii) delay sowing until temperatures are warm enough to promote rapid germination and (iv) sowing as few seeds as possible per container cavity or as far apart as practical in bareroot drills. Probably the most practical recommendation is to add a suitable fungicide to the stratification water or dust the seeds with it before sowing (Gordon and others 1976; Salt 1974).

Sirococcus Blight

This disease, caused by the fungus Sirococcus strobilinus Preuss, affects conifer regeneration and forest nursery seedlings throughout the North Temperate Zone (Sutherland and others 1981A; Wall and Magasi 1976 and references cited therein; Wicker and others 1978 and references cited therein). Occasionally, minor damage occurs on older forest trees, e.g. western hemlock, Tsuga heterophylla (Raf.) Sarg.,(Funk 1972). Sirococcus blight is especially troublesome on both regeneration and nursery seedlings along those portions of the North American west coast where cooler, wet and often overcast weather favors the disease. Local hosts are spruces, e.g., white, Engelmann, Picea engelmannii Parry, Sitka, P. sitchensis (Bong.) Carr., pines such as lodgepole and yellow, Pinus ponderosa Laws., Douglas-fir and western hemlock.

In 1981 it was shown that S. strobilinus is seed-borne on spruces (Sutherland and others 1981A); subsequent observations (J.R. Sutherland and W. Lock, unpublished) indicate that it also may be seed-borne on western hemlock and yellow pine, but not lodgepole pine (Sutherland and others 1982). While the pathogen has been found on seedcoats, it normally penetrates seeds and ramifies throughout the contents (Sutherland and others 1981A) so that diseased seeds do not germinate. However, in container nurseries these dead seeds serve as inoculum for adjacent seeds which apparently acquire the fungus, germinate and emerge, then become diseased. These diseased seedlings are foci for subsequent spread of the fungus via splashing irrigation water. The situation seemingly is different in bareroot nurseries where the fungus appears to be unable to bridge the gap between diseased and healthy seeds, i.e., the latter do not acquire the pathogen before germinating. At least two factors are thought to allow the bridging in containers. Firstly the medium is probably more conducive (less microbial competition?) to Sirococcus and secondly, container seeds are sown more densely with frequently two or more seeds being sown per cavity. The latter practice also increases the likelihood of placing a diseased seed in a cavity. Sirococcus blight of bareroot seedlings can originate from inoculum in wind-blown rain (Riffle and Smith 1979), such as from nearby windbreak trees, or from inoculum on cones which fall into seedbeds (Srago 1978). Observations leading to the suspicion that S. strobilinus was seed-borne were that the disease first appeared on very young germinants of specific seedlots over several years and that the fungus is common on cones, particularly spruce.

Sirococcus blight damage and symptoms are well known on seedlings (Smith 1975; Sutherland and Van Eerden 1980) and regeneration (Wicker and

others 1978). Funk (1981) summarizes information on the pathogen such as spore size and shape. These references will be useful to persons collecting cones from natural stands. Seed orchard managers likely will not have to deal with the disease on either cones or trees, mainly because orchard cones are collected each year which removes an important source of inoculum. In nature the fungus is thought to build up on old cones that remain on trees and when these are inadvertently included in collections they are a major source of Sirococcus-infested seeds (J.R. Sutherland and T.A.D. Woods, unpublished). Another reason Sirococcus blight is unlikely to be important in seed orchards is that prolonged light stress, a major factor predisposing hosts to the pathogen (Wall and Magasi 1976), seldom occurs in orchards.

Seed-borne Sirococcus is another example of a problem created by poor cone collection practices, i.e. by including diseased cones in collections. Old cones are most likely to be diseased. This problem is difficult to overcome because late in the collection season it is extremely difficult to distinguish current year from old cones. Presence of S. strobilinus fruit bodies on cones indicates that the seeds will be infested, but laboratory confirmation is necessary because other similar-appearing fungi also fruit on cones. Attempts to remove Sirococcus-diseased seeds by repeatedly cleaning infested seedlots with air or by passage over a gravity table have been unsuccessful (J.R. Sutherland and W. Lock, unpublished). In container nurseries, benomyl or daconil fungicide drenches after sowing Sirococcus-infested spruce seedlots has produced conflicting results for disease control and the trials need repeating (G. Matthews, personal communication). In B.C., recommendations for container nurseries are to warn managers when infested seedlots are being sown so that fungicide spraying, and when practical, roguing diseased seedlings, can begin when the disease appears. Withholding watering or watering in the morning so that seedlings dry off quickly also helps alleviate damage. A disadvantage of fungicides is that they must be applied frequently to protect rapidly expanding tissues and this leads to fungicide accumulation on seedlings which concerns nursery workers and tree planters. Also, fungicides applied early in the season against Sirococcus may lead to build up of fungicide tolerance in late season pathogens such as Botrytis cinerea.

Other Cone and Seed Fungi

Besides the previously mentioned fungi and the Fusaria that Dr. James is covering in his paper, many other fungi have been reported in and on cones and seeds of local tree species (Bloomberg 1969; Harvey and Carpenter 1975; Rediske and Shea 1965; Richardson 1979; Richardson 1981; Shea 1960). Many of these are potential pathogens to cones, seeds or seedlings while others such as Heterobasidion annosum (Fr.) Bref. (Richardson 1979; Richardson 1981), which causes a butt rot of older trees, are obviously incidental. The real gray area in our knowledge concerns the role of the most common and so-called saprophytic fungi such as Penicillium and Aspergillus that have been found on cones and especially seeds. Most research on these fungi has been of a single, short-term nature and the results and interpretations to date are conflicting. Consequently few conclusions can be drawn from the literature.

Another shortfall is that since none of the studies have fulfilled Koch's Postulates it is impossible to establish a cause and effect relationship for any of these fungi. Although cones and in turn seeds apparently acquire these various fungi while still on the tree, there is no evidence that fungus development occurs until the cones have ripened and are collected. Numerous fungi can then develop on the stored cones prior to seed extraction, but mold incidence and abundance on cones appears not to subsequently affect seed quality (Bloomberg 1969). It is only after seed extraction and particularly during germination tests that molds appear (Bloomberg 1969). At least in Douglas-fir, the low percentage of healthy, non-germinable seeds indicates that the fungi and possibly bacteria are facultative parasites of low quality seeds (Bloomberg 1969). Based on our limited knowledge this seems to be true for seeds of other conifers too, e.g. reducing the abundance of molds on Abies seeds failed to increase germination (Edwards and Sutherland 1979). Examples of factors that can lower seed quality and thereby increase susceptibility to these facultative parasites include both internal and seed coat damage acquired during extraction from cones, insect damage, and probably most importantly, lack of maturity (Bloomberg 1969). The low temperatures and low moisture content of both seeds and the environment inhibit mold development in long-term storage (Holmes and Buszewicz 1958). However, in the local context nothing is known about what happens afterward during seed stratification or subsequently when seeds are stored before sowing. Present evidence indicates that incidence and abundance of so-called saprophytic fungi such as Aspergillus and Penicillium are indicators rather than the cause of poor quality seeds.

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DISEASES OF CONIFER SEEDLINGS CAUSED BY SEED-BORNE FUSARIUM SPECIES

R. L. James

ABSTRACT: The genus Fusarium includes many common soil-borne fungi that may colonize conifer seed, especially if cones are collected from the ground or squirrel caches. These fungi most commonly infect the seed coat, but can also colonize the seed embryo and endosperm. Fusarium spp. cause a wide variety of diseases, most of which affect the roots of susceptible plants. Types of diseases commonly affecting conifer seedlings in nurseries include (1) seed decay, (2) pre-emergence damping-off or germination failure, (3) postemergence damping-off, (4) topdamping-off or cotyledon blight, and (5) root diseases or late damping-off. The most common species of seed-borne fusaria include F. oxysporum, F. solani, F. moniliforme, and F. "roseum." Diseases caused by Fusarium can be reduced by seed treatments such as running water rinses, surface sterilants, and fungicides.

INTRODUCTION

Conifer seeds are storehouses of food and energy and many microorganisms have evolved mechanisms for invading and utilizing them. Many different fungi commonly infect conifer seeds. Infection frequently damages seed and also provides a means by which fungi may be transferred from one substrate or geographic location to another (Harman 1983).

Fusarium spp. are common soil-inhabiting plant pathogens (Booth 1971; Gerlach and Nirenberg 1982), which also frequently infect conifer seed (Neergaard 1977). These fungi attack a wide range of hosts and cause economically important diseases of many commercial crops, including conifer seedlings (Bloomberg 1971; Tint 1945). Fusarium spp. commonly occur within many types of soils. Populations frequently increase in cultivated soils (Booth 1971); low levels of these fungi often occur in undisturbed natural soils (Smith 1967).

Fusarium diseases of conifer seedlings have traditionally been most important in bareroot nurseries (Bloomberg 1971). Pathogen populations are often reduced in nursery soils by using fumigants such as methyl bromide and chloropicrin (Miller and Norris 1970). However, Fusarium-caused diseases sometimes occur despite soil fumigation (Cooley 1982). Investigations of diseases incited by Fusarium indicate that these fungi may be introduced into both bareroot and container nurseries on conifer seed, causing extensive losses (Cooley 1983b; Graham and Linderman 1983; James 1983a).

Although Fusarium spp. can infect conifer seed during flowering and cone formation, (Anderson and others 1980; Mason and Van Arsdel 1978; Sharma 1978), probably most infection occurs when cones or seed contact soil that harbors inoculum (James 1983c; Karrfalt 1983). Cones collected from squirrel caches often contain large populations of fungi including many pathogenic fusaria (James 1984c; James and Genz 1981; James and Genz 1982). During the seed extraction process, infection by fusaria may intensify (Salisbury 1955), resulting in both seedcoat and endosperm colonization (James 1984b; James 1984c). Diseases of seeds often increase during prolonged seed and cone storage (Bloomberg 1969; Harmon and others 1978; Harvey and Carpenter 1975). Seed colonization by pathogens can also increase during the extended seed stratification periods that are common in conifer nurseries (Bloomberg and Trelawny 1970).

TYPES OF DISEASES

Fusarium spp. cause several different kinds of diseases, the most important of which affect roots of susceptible plants (Booth 1971; Gerlach and Nirenberg 1982). Five types of diseases caused by these fungi are generally recognized on conifer seedlings. These include seed decay, pre-emergence damping-off or germination failure, postemergence damping-off, top damping-off or cotyledon blight, and root disease or late damping-off (Bloomberg 1971; Matuo and Chiba 1966).

Seed decay occurs when fungi penetrate the seedcoat, colonize it and break down internal seed contents (Bloomberg 1969). Seeds with damaged seedcoats are especially vulnerable to rapid fungal invasion (Gibson 1957; Neergaard 1977). Decayed seed may or may not be detectable from outward appearance (Bloomberg 1966). However, x-rays, which reveal hollow or partially deteriorated endosperms, can aid detection (Anderson and others 1980). Decayed seed may also be detected during water or air separation operations because of their reduced densities (James and Genz 1981; James and Genz 1982; Neergaard 1977). If decayed seed are sown, decreased germination will result and potentially pathogenic fungi are introduced into seedbeds or containers (James 1984a; Landis 1976a).

Pre-emergence damping-off occurs when the emerging radicle of germinating seed is attacked by fungi either carried on the seedcoat or present in soil (Bloomberg 1971; Graham and Linderman 1983). If the radicle is colonized by virulent fungi, decay results and no germinant emerges (Rathbun-Gravatt

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1931). Most losses to pre-emergence damping-off are never detected and are often attributed to "bad seed." Investigations of nonemergence of germlings are usually necessary to determine if pathogenic fungi are involved.

Postemergence damping-off refers to disease of newly emerged germinants. Lesions often appear at the ground line, causing infected germinants to fall over (Bloomberg 1971; Landis 1976a). Decay of the germinant follows and sporulation may occur on decayed tissues. Seed-borne fusaria may incite postemergence damping-off, resulting in reduced seedling densities (Graham and Linderman 1983; Matuo and Chiba 1966; Urosevic 1961).

Top damping-off caused by Fusarium spp. occurs as colytedon blight (Mason and van Arsdel 1978), hypocotyl rot (Brownell and Schneider 1983; Hamm, personal communication), or stem rot (Morgan 1983). Cotyledon blight is especially common on pine species that retain their seedcoats on the tips of cotyledons for extended periods after germination (Mason and van Arsdel 1978). Seed-borne fusaria move from attached seedcoats and colonize cotyledons, causing decay and eventual mortality. Hypocotyl and stem rots are caused by either natural populations of soil-borne fusaria or pathogens introduced on infected seed.

Root disease caused by Fusarium usually occurs on seedlings that are several months old. Disease results from decay of feeder roots (Pawuk and Barnett 1975); affected seedlings become slow growing and chlorotic (Landis 1976b) and may develop wilt symptoms and needle tip dieback (James 1983a; James 1984c; James 1984d). Seedling deterioration may occur either gradually or rapidly (Merrill and others 1981). The disease may cause seedling mortality or reduced seedling vigor, which adversely affect outplanting survival (LaMadeleine 1979). Seedlings may become infected during or shortly after establishment, but infecting fungi may remain inactive for several months (Bloomberg 1966). When seedlings become stressed during crown closure, periods of heat or moisture stress, or during hardening off, the infecting fungi may become active and induce disease (James 1984c; James 1984d). Another possibility is that soil-borne fusaria may become more pathogenic when seedlings are stressed. In any event, losses from root disease can continue for several months in containerized stock (James 1983c; Landis 1976b) and throughout the first and second growing seasons in bareroot stock (James 1983b; James 1983d).

SPECIES OF FUSARIUM

The most common species of Fusarium isolated from conifer seed is F. oxysporum Schlect. (Graham and Linderman 1983; James 1984b; James 1983c; James and Genz 1982). This fungus is an important seed- or soil-borne pathogen of many different plants including conifer seedlings (Booth 1971; Cooley 1983a; Gerlach and Nirenberg 1982). It is capable of causing vascular wilts (Booth 1971; Neergaard 1977) and cortical rots of seedling stems (Brownell and Schneider 1983; Morgan 1983) and roots (James 1984b; James 1983d). Although F. oxysporum exhibits a wide host range (Booth 1971; Gerlach and Nirenberg 1982) individual strains of the fungus, called formae specialis (f. sp.), usually infect only a few selective hosts (Gordon 1965; Snyder and Hansen 1940). Only one f. sp. (designated pini) is usually recognized for isolates of F. oxysporum that attack conifers (Gordon 1965).

Isolates that cause diseases of conifers are generally not thought to infect other plant species (Brownell and Schneider 1983). However, responses of different conifer species to infection by several F. oxysporum isolates have sometimes been sufficiently variable to indicate that designation of additional f. sp. (other than pini) which attack conifers might be warranted (James and Gilligan 1984; Matuo and Chiba 1966). Additional pathogenicity tests on a wide range of conifer hosts will be needed to help clarify this issue. Pathogenic isolates of F. oxysporum have been obtained from conifer seed (Graham and Linderman 1983). However, nonpathogenic isolates have also been frequently isolated. Therefore, occurrence of F. oxysporum on seed does not necessarily mean that disease will result (James 1984a; James and Genz 1982).

Another Fusarium species commonly isolated from conifer seed is F. solani (Mart.) Sacc. (James 1983a; James 1983c; James 1984a). It is a common root decay organism that is especially damaging on certain agricultural crops (Booth 1971; Gerlach and Nirenberg 1982; Neergaard 1977). The fungus is occasionally associated with diseases of conifer seedlings (Landis 1976b; Merrill and others 1981; Tint 1945). However, the pathogenic potential of seed-borne sources of this fungus is unclear for conifer seedlings.

Other species of Fusarium frequently isolated from conifer seed include F. moniliforme Sheldon and F. roseum (Lk.) Sacc. (James 1983c; James 1983e; James 1984a; James and Genz 1982). Fusarium moniliforme causes root decay in several types of plants (Booth 1971; Gerlach and Nirenberg 1982), but is infrequently associated with conifer diseases (James 1984a; Rowan 1982). Fusarium roseum is actually a complex of organisms that produce distinctive pigments in culture (Booth 1971). Members of this group are frequently isolated from conifer seed (James 1983c; James 1983e; James and Genz 1981) and less frequently from diseased seedlings (James 1983; James 1984d; Morgan 1983). Although some of these fungi may be pathogenic (James and Gilligan 1984; Morgan 1983), most are saprophytic (Booth 1971; Gerlach and Nirenberg 1982). Seed-borne isolates of F. roseum have generally not been evaluated for their pathogenic potential.

DISEASE CONTROL

The extent of Fusarium contamination on seed varies greatly among conifer species and seedlots (James 1984a; James and Genz 1982). Differences among seedlots may be related to cone collection, storage and seed extraction practices. Cones collected from squirrel caches often have high levels of fungal contamination. Also, cones and seed stored under

damp conditions for longer time periods are more prone to damage by fungi.

Seed treatment before sowing may reduce disease losses caused by seed-borne fusaria (Johnson and Harvey 1975; Johnson and Linton 1942). Most growers soak seed in water to condition them for sowing; some use standing water and others a running water rinse (James 1984a). If infected seed is soaked in standing water, fungal propagules can spread, causing widespread infection (James 1983e). However, placing seed under a running water rinse can reduce seedcoat contamination and does not spread infection (James 1983e; James 1984a).

Surface sterilants, such as hydrogen peroxide and sodium hypochlorite (commercial bleach), have frequently been used to reduce fungal contaminations and enhance germination of conifer seed (Advincula and others 1983; James and Genz 1981). Hydrogen peroxide usually reduces or eliminates fungal contaminants (Barnett 1976; James and Genz 1981). The effect of hydrogen peroxide on conifer seed germination has been variable. For example, some investigators (Edwards and Sutherland 1979; James 1983a) report reduced seed germination; others (Ching and Parker 1958; James and Genz 1981; Mason and van Arsdel 1978) report improved germination. Detrimental effects of H_2O_2 generally increase with chemical concentration and exposure period. Sodium hypochlorite usually reduces fungal contamination (James and Genz 1981) and sometimes enhances seed germination (Advincula and others 1983).

Several fungicides have been used for seed treatments to reduce damping-off caused by seed-borne pathogens (Mittal and Sharma 1981; Strong 1952); however, reports of fungicide toxicity to seed and germinants have limited their use (Cooley 1983a; James 1983e; Lock and others 1975). For example, use of captan has resulted in reduced seed germination (Peterson 1970), and has caused seedling injury following germination (Cayford and Waldron 1967; Lock and others 1975). Thiram, another common seed-treatment fungicide, has reduced seed germination (Dick and others 1958; Shea 1959) and caused deformed germinants (Hedderwick and Gadgil 1966). Effectiveness of seed-treatment fungicides is apparently related to dosage levels (Hamilton and Jackson 1951), activity spectrum against target organisms, development of resistant fungal strains, and persistence on seed (Sutherland and van Eerden 1980).

CONCLUSIONS

1. The genus Fusarium causes a wide variety of diseases of conifer seedlings.

2. Several Fusarium spp. have been shown to be carried both externally and internally by conifer seed.

3. The best method to reduce Fusarium contamination of seed is unclear, although running water rinses may be effective.

4. Seedlots of susceptible species should be bioassayed for presence of Fusarium after extraction to identify problem lots.

RESEARCH NEEDS

Effects of cone collection, storage, and seed handling techniques on disease caused by seed-borne fusaria need investigation. Several pertinent questions need to be answered, for example, should squirrel cache collections be permitted for susceptible species, and should cones be stored under specific conditions to reduce spread of Fusarium? What are the best temperatures and seed moisture levels for storage of Fusarium-infested seedlots? Should infested seedlots be stratified? Will stratification improve or reduce germination?

Another important research need concerns taxonomy of F. oxysporum strains that cause diseases of conifer seedlings. Pathogenicity tests on a wide range of conifer hosts are needed to determine host specificity characteristics of fungal strains.

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MONOCLONAL ANTIBODIES RECOGNIZING THE SEED-BORNE FUNGAL PATHOGEN Sirococcus strobilinus

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ABSTRACT: Hybridoma cell lines producing monoclonal antibodies (McAbs) recognizing antigens of the seed-borne conifer pathogen, Sirococcus strobilinus have been prepared by cell fusion techniques. Specificity of these McAbs has been ascertained in enzyme-linked immunosorbent and surface immunofluorescence assays using a panel of nonrelated commensal fungi. These McAbs will serve as reliable diagnostic probes in assaying seeds for S. strobilinus.

INTRODUCTION

Sirococcus shoot blight caused by the fungus, Sirococcus strobilinus Preuss (syn. Ascochyta piniperda Lindau) is an important seed-borne disease in coastal British Columbia container nurseries where it affects Sitka and white spruce (Sutherland and others 1981). The pathogenesis of Sirococcus blight and its confinement to specific spruce seedlots are indicative that the disease is seed-borne and recently this was confirmed by Sutherland and others (1981).

Current methods for detecting seed-borne pathogens such as S. strobilinus involve plating surface sterilized seeds onto nutrient media and identifying fungal outgrowth on the basis of general morphology and the production of distinctive spores. These techniques are time-consuming and insufficiently sensitive for detecting low levels of pathogens. The success of Sirococcus detection by these methods is low (0.5 to 3 percent) as often rapidly growing saprobes mask the slower-growing Sirococcus. Also, as Sirococcus often fails to sporulate in culture, definitive identification based on spore morphology is not always possible. However, the consequences of failure to diagnose Sirococcus infestation in a seedlot are often severe as nursery conditions are highly favorable to the disease. Thus, a more reliable test for this pathogen is needed. The specificity, speed and relative economy of an immunoassay would fulfill these requirements.

The primary requisite of such an immunologic test is specific antibody to serve as a probe for locating Sirococcus strobilinus components (antigens) in or on seeds. Techniques devised by Köhler and Milstein (Köhler and Milstein 1975; Milstein 1980) permit the isolation of cells which produce antibodies of unique specificities (called monoclonal antibodies). In this procedure, antibody-forming cells taken from the spleen of a mouse that has been immunized with antigen are fused to cancerous myeloma cells to form new cells (called hybridomas) which have the ability to live indefinitely in culture and to produce and to secrete into the culture fluids monoclonal antibodies (McAbs) directed to the antigen.

This paper describes the derivation, by cell fusion techniques, of hybridoma cell lines which produce McAbs recognizing antigens of S. strobilinus. The McAbs recognize antigens from several S. strobilinus isolates obtained from diverse host species and tissues but do not react with other nonrelated seed-associated fungi when tested in enzyme-linked immunosorbent (ELISA) or by indirect surface immuno-fluorescence (IFA) assays and thus will be useful diagnostic probes for Sirococcus in seeds and other tissues.

MATERIALS AND METHODS

Fungal Isolation and Culture

Axenic cultures of Sirococcus strobilinus and 10 other saprophytic fungi isolated from surface-sterilized (Sutherland and others 1978) seeds obtained from an Engelmann spruce (Picea engelmanni Parry) seedlot were prepared as previously described (Sutherland and others 1981). Fungi used for immunizing mice or for the preparation of soluble antigens were grown in 1.25% malt extract broth (MB) containing trace amounts of B, Cu, Fe, Mn, Mo and Zn (Vézina and others 1965).

Preparation of Fungal Antigens

Antigens for immunizing mice and for testing McAbs were prepared as follows. Mycelium from axenic cultures of S. strobilinus and commensal fungi, grown in MB, was separated from the culture medium, washed with 100 mL of distilled water by vacuum filtration and used directly or frozen at -20°C.

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Total antigens.--Mycelium (5-10 g) was homogenized immediately in a volume of 3-4 mL of phosphate buffered saline (PBS, pH 7.4 containing 10 mM Na and K phosphates, 3 mM KCl and 140 mM NaCl) in a glass homogenizer, then dried for 24 hr at 40°C in glass Petri dishes. The dried mycelium was scraped from the Petri dish, ground into a fine powder and stored at 4°C.

Soluble antigens.--Five to 10 g of frozen mycelium was suspended in 20 mL of extraction buffer (50 mM NH_4HCO_3/2% w/v polyvinylpyrrolidone) and homogenized for 2 min at maximum speed in a polytron homogenizer (Type PT 20-OD, Kinematica, Lucerne, Switzerland). The disrupted mycelium was held at 0°C for 1 hr, rehomogenized, then centrifuged for 20 min at 600 x g. The supernatant was saved and the pellet re-extracted twice with 15 mL of extraction buffer. Supernatants from all extractions were pooled, cleared by centrifugation at 12000 x g and stored -20°C. Protein concentrations were determined as described by Lowry and others (1951).

Secreted antigens.--Antigens secreted into culture fluids were prepared by mixing two volumes of 95% ethanol with one volume of filtered culture fluids. Precipitation was allowed to occur for 24-48 hours at 4°C then the mixture was centrifuged for 30 min at 10000 x g and the pellet redissolved in 10-20 mL of distilled water and stored at -20°C.

Animals

BALB/c mice were obtained from Charles River (Canada) Inc., St. Constant, Que, or bred from parental stock purchased from the same source. Both male and female mice, aged 6-12 weeks were used.

Immunization of Animals

Mice were immunized by intraperitoneal (i.p.) injection of 5 mg of air-dried mycelium emulsified with Freund's complete adjuvant in a volume of 0.2 mL/animal and challenged five times at 4-6 week intervals by i.p. injection of 1 mg of mycelium in Freund's incomplete adjuvant in the same volume. Three days before cell fusion mice were given 0.1 mL of S. strobilinus soluble antigens intravenously.

Sera from mice hyperimmunized with S. strobilinus dried mycelium were pooled and used as positive reference sera in enzyme-linked immunosorbent and immunofluorescence assays as described below. Sera pooled from another group of animals immunized in the same way with air-dried mycelium from Trichoderma viride (a common saprophyte on seeds) served as a negative reference serum.

Enzyme-linked Immunosorbent Assays (ELISAs)

Enzyme-linked immunosorbent assays were performed as described by Voller and others (1976) with the following modifications. Wells of 96 well, flat-bottomed polystyrene microtiter plates (no. 3590 Serocluster, Costar, Cambridge, MA) were coated with 50 µL/well of fungal soluble antigens adjusted to a protein concentration of 10µg/mL in distilled water. The plates were dried overnight at 37°C, then well sites not coated with antigen were blocked by adding 200 µL of 1% bovine serum albumin (Fraction V) in PBS (pH 7.4) to each well and incubating for 2 hr at room temperature. All other aspects of the assay were conducted as described by Voller and others (1976) using 50 µL volumes/well of hybridoma culture fluids or dilutions of ascites fluids in the first antibody layer and the same volumes of optimal dilutions of enzyme-labelled second antibody. Enzyme-labelled second antibodies employed were anti-mouse IgF(ab')$_2$-alkaline phosphatase conjugate (Helix Biotech, Vancouver, B.C.) or anti-mouse IgG (H + L)-peroxidase conjugate (HyClone Labs., Logan, UT) which were used to detect antibodies of all classes. Alkaline phosphatase-labelled chain-specific second antibodies, anti-mouse IgM (µ-chain) and anti-mouse IgG (γ-chain) were used to detect antibodies of the IgM and IgG classes, respectively. All second antibodies were affinity-purified and no binding to Sirococcus or other fungal antigens was observed in the absence of specific antibody. In assays where alkaline phosphatase-labelled second antibodies were employed 4-nitrophenyl phosphate (Boehringer-Mannheim, Dorval,Que.), 1 mg/mL in diethanolamine buffer pH 9.8 (0.97% v/v diethanolamine containing 0.02% NaN_3 and 0.1 mg/mL $MgCl_2.6\ H_2O$) was used as the substrate. The enzymatic reaction was allowed to proceed for 45 min in the dark at room temperature then stopped by adding 50 µL/well of 3 M NaOH and A_{405} was determined for each well with a MicroELISA Minireader (Series MR 590, Dynatech, Alexandria, VA). In assays where peroxidase conjugate was used the substrate solution consisted of o-phenylenediamine (Fisher, Vancouver, B.C.), 0.4 mg/mL and 3% H_2O_2, 4 µL/mL (v/v) in citrate buffer (pH 5.0). The microplates were incubated in darkness for 15 min at room temperature. The enzymatic reaction was stopped by adding 50 µL of 2.5 M H_2SO_4 to all wells and A_{490} was determined for each well.

Indirect Immunofluorescence Assays (IFA)

Unit layers of mycelium were grown on acid washed sterile 18 mm² glass coverslips (mounted on autoclaved filter paper disks moistened with MB in covered Petri dishes) by inoculating them with 1 drop of medium from sporulated cultures. When hyphae were visible the coverslips were removed individually to 60 mm glass Petri dishes and washed with 5 mL PBS containing 10% fetal calf serum (FCS) for 15 min at room temperature. The PBS/FCS was suctioned off and replaced with 100 µL of undiluted culture fluids and incubated in a moist chamber at room temperature for 1 hr. The coverslips were washed with 10 mL PBS/FCS and suctioned

dry. One hundred µL of fluorescein (FITC)-conjugated second antibody (anti-mouse IgG or anti-mouse IgM chain-specific sera, Kirkegaard and Perry, Gaithersburg, MD diluted to 1/20 in PBS/FCS and centrifuged for 5 min at 12000 x g) were added to each coverslip and incubated for 1 hr at room temperature. The coverslips were washed as before and inverted onto glass slides with 1 drop of mounting medium (90% glycerol in PBS, with 1 mg/mL o-phenylenediamine). The slides were examined with a Zeiss Photoscope II equipped with a 100 illuminator (fitted with an HBO 50 W high pressure Hg source), epifluorescence condenser III RS, 390-440 nm excitation and 475 nm barrier filters, 10x and 40x Neofluar objectives and 10x Kpl-w eyepieces.

Derivation of Hybridomas

Media and supplements.--RPMI-1640 medium, glutamine (200 mM), gentamycin (50 mg/mL), 4-(2-hydroxyethyl)-1-piperazine ethanesulfonic acid (HEPES, 1 M) were obtained as sterile solutions from Gibco Canada Ltd., Burlington, Ont. Sodium pyruvate, 2-mercaptoethanol, hypoxanthine, aminopterin, thymidine, dimethylsulfoxide (DMSO) and 2, 6, 10, 14-tetramethylpentadecane (Pristane) were obtained from Sigma, St. Louis, MO. Polyethylene glycol (Serva 1550) was from Terochem Labs., Edmonton, Alta. Fetal calf serum (FCS), preselected for its ability to support optimal growth of the myeloma cells used in fusion (see below) was supplied by Animal Health Labs., Islington, Ont. FCS was heat-activated (56°C for 30 min) prior to use as a medium supplement.

Myeloma cells.--SP2/0-Ag14, a nonsynthesizing myeloma cell line of BALB/c mouse origin (Shulman and others 1978) was obtained from Dr. T.W. Pearson (Department of Biochemistry and Microbiology, University of Victoria, B.C.). Prior to their use in cell fusion, the cells were grown for several passages in log phase in growth medium consisting of RPMI-1640 supplemented with 10% FCS, 0.5 mg/mL gentamycin, 2 mM glutamine, 1 mM Na puruvate and 0.1 mM 2-mercaptoethanol.

Cell Fusions.--Media, supplements and solutions used in cell fusion were prepared as described by Pearson and others (1980). All procedures were carried out under aseptic conditions. BALB/c mice that had been hyperimmunized with dried mycelium and rechallenged by intravenous injection of soluble antigens from S. strobilinus were used as spleen cell donors. Spleens were dispersed into single cell suspensions in fusion medium consisting of RPMI-1640 medium supplemented with 20% FCS, 0.5 mg/mL gentamycin, 2 mM glutamine, 1 mM Na pyruvate, 0.1 mM 2-mercaptoethanol and 10 mM HEPES, washed twice by centrifugation at 500 x g for 10 min at 4°C and adjusted to 1×10^7 or 2×10^7 cells/mL in the same medium. Log phase SP2/0 cells were washed once by centrifugation and adjusted to 1×10^6 or 2×10^6 cells/mL in fusion medium. Immune spleen cells and myeloma cells were mixed at a ratio of 10:1 and fused in the presence of polyethylene glycol as described by Pearson and others (1980). The fused cells were immediately dispensed in 50 µL aliquots into wells of 96 well microculture plates (no. 25860, Corning, Palo Alto, CA), supplemented with 160 µL/well of fusion medium containing 6.25×10^4 normal BALB/c mouse thymocytes as feeder cells and cultured for 18 hr at 37°C in 10% CO_2 in air. At the end of this period, the medium was removed and replaced with 150 µL/well of selective medium (HAT medium, consisting of fusion medium with 13 µg/mL hypoxanthine, 0.2 µg/mL aminopterin and 3.9 µg/mL thymidine). The microplates were returned to the incubator and fresh HAT medium added to the wells on days 7 and 14 after cell fusion. During this period the microplate wells were checked frequently for cell growth. When colonies were visible, culture fluid from each well was tested in ELISA for specific antibody. The contents of wells producing Sirococcus-specific antibody were removed to 1 mL of HT medium (fusion medium supplemented with 13 µg/mL hypoxanthine and 3.9 µg/mL thymidine) containing 1×10^6 thymocytes/mL in 24 well culture plates (no. 3524, Costar). After cell expansion, antibody specificity was checked by testing the medium in each well in ELISA using soluble antigens from either Sirococcus or Trichoderma. Hybridoma cells from wells that were positive for Sirococcus but negative for Trichoderma were cloned by limiting dilution as described below.

Limiting Dilution Cloning of Hybridomas

Hybridomas were cloned twice by diluting cells to 80, 20 and 10 cells/mL in cloning medium consisting of HT medium (first cloning) or fusion medium (second cloning) with 1×10^6 thymocytes/mL. For each dilution, 0.1 mL/well was pipetted into 12 wells of microculture plates to give cell densities of 8, 2, and 1 cell/well, respectively. After incubation at 37°C in 10% CO_2 in air for 7-14 days, wells were screened for specific antibody production and selected clones were expanded and cryopreserved or injected into mice for ascites production as described below.

Freezing and Thawing of Hybridomas

Hybridoma cells obtained from log phase culture were adjusted to 2×10^6 to 1×10^7 cells/mL in 90% FCS/10% glycerol and cryo-preserved in 1 ml aliquots in liquid nitrogen. To re-establish hybridomas in culture, the cells were thawed rapidly in a 37°C water bath and immediately centrifuged through 10 mL of warmed fusion medium. Cells were resuspended in 3-5 mL of the same medium in 25 cm^2 culture flasks which were gassed with 5% CO_2 in air, sealed and incubated as described above.

Production of Ascites

For production of ascites tumors, 1-2 x 10^7 hybridoma cells in a volume of 0.2 mL were injected i.p. into BALB/c mice primed (by i.p. injection) 10 days previously with 0.5 mL of Pristane. Ten to 14 days later the animals were killed and the ascites fluids removed aseptically from the peritoneal cavity. Cells were pelleted by centrifugation at 500 x g for 10 min at 4°C and cryopreserved as described above. The supernatant was filtered through cotton wool then stored in 0.2 mL aliquots at -20°C.

RESULTS

Derivation of Hybridoma Cell Lines Producing Monoclonal Antibodies Directed to *Sirococcus strobilinus*.

Two independent cell fusions (SDM1 and SDM2) were conducted using different spleen cell (SPLC) and myeloma cell (SP2/0) cell densities as described in Methods. Macroscopic colonies were visible in microculture plate wells within 7 days and culture fluid from each well was tested for specific antibody by ELISA 11 days after fusion. In fusion SDM1 in which SPLC and myeloma cells were mixed at a ratio of 1 x 10^7:1 x 10^6, 31 wells out of 480 contained antibody-producing hybidomas. The second fusion (SDM2) conducted at higher SPLC:myeloma cell densities (2 x 10^7:2 x 10^6) resulted in 7/480 wells which were positive for antibody production.

Cells producing specific antibody were expanded in 24 well culture plates and five days later, culture medium from each well was tested for specific antibody in ELISA using soluble antigens from *S. strobilinus* or *Trichoderma viride* or extraction buffer to coat ELISA plate wells. In 11 of the wells tested, antibodies in the culture fluids bound only to *Sirococcus* antigens, while in nine of the wells, antibodies which bound to both *Sirococcus* and *Trichoderma* antigens as well as extraction buffer-coated wells, were present. Those cells producing antibodies which recognized only *Sirococcus* soluble antigens were cloned twice by limiting dilution. After each cloning, hybridoma cells were tested for specific antibody production by ELISA. As a result, 30 stable cloned hybridoma cell lines producing *Sirococcus*-specific monoclonal antibodies (McAbs) were established. These cell lines are clones originating from five different (parental) wells in the initial fusion plates (indicated by the numbers 475, 441, 434, 171 and 392 in table 1). For each line, cells were cryopreserved in liquid nitrogen and McAb isolated from culture or ascites fluids. Twelve of the hybridoma lines (of the series 441 and 171) produce McAbs of the IgM class, while 18 (series 434, 475 and 392) hybridoma lines produce IgG McAbs as determined in ELISA using chain-specific second antibodies.

Analysis of Monoclonal Antibody Specificity

Antigen recognition in other Sirococcus strobilinus isolates.--As the primary goal of producing *S. strobilinus*-specific McAbs was to develop a diagnostic reagent for detecting this

Table 1.--Reactivity of *Sirococcus*-directed monoclonal antibodies with soluble antigens from other *Sirococcus strobilinus* isolates

Sirococcus isolate	Host[2]	A_{490} nm/Hybridoma[1] SDM 1/475.6a.9	SDM 1/441.4.4	SDM 1/434.15.21	SDM 1.171.27.13	SDM 2/392.2.4
2456	ES	2.00	2.00	2.00	2.00	2.00
8652	SS	1.33	0.39	0.35	2.00	1.25
2231	SS	2.00	0.74	2.00	1.67	0.27
8615	WS	1.41	1.96	0.49	2.00	1.92
4321	IS	1.55	2.00	0.39	2.00	1.79
RR	LP	1.75	1.85	0.73	2.00	0.79
2311	LP	2.00	1.11	0.71	2.00	0.42
4248	LP	1.46	1.19	1.44	2.00	1.15
2247	WH	0.46	0.00	0.00	1.89	0.08

[1] McAbs produced by SDM hybridoma cell lines were tested in ELISA using soluble antigens (at 10 µg/mL) prepared from the isolate used in their derivation (2456) and eight other *S. strobilinus* isolates, to coat ELISA plate wells. A positive A_{490} nm value indicates reactivity of the McAb with its antigen in the soluble antigen mixture.

[2] ES = Engelmann spruce, SS = Sitka spruce, WS = white spruce, IS = Interior spruce, LP = Lodgepole pine, WH = western hemlock.

pathogen in seeds, it was important to ensure that the McAbs were not isolate-specific. Therefore, culture fluids obtained from each hybridoma line were tested in ELISA using soluble antigens prepared from nine different isolates of S. strobilinus from several host species and tissues. The results of assays done on representative clones of each parental cell line are shown in table 1. The results obtained with McAbs from other clones within each parental line were similar. Thus, the McAbs produced by the hybridomas collectively recognized antigen(s) present in all the Sirococcus isolates tested. However, differential patterns of reactivity were observed with different Sirococcus isolates and McAbs originating from different parental lines.

Specificity of monoclonal antibodies for Sirococcus strobilinus.--As Sirococcus is frequently associated with nonpathogenic fungi in or on seeds, it was necessary to ensure that the McAbs did not recognize antigens common to Sirococcus and other saprobes. Therefore, the McAbs were tested in ELISAs using soluble antigens prepared from Sirococcus or soluble antigens from seven different genera of commensal fungi all isolated from the same infested seedlot (2456) to coat microtiter plate wells. The results (table 2) showed that all McAbs were specific for S. strobilinus antigens and did not crossreact with antigens from commonly found saprophytic fungi. Although all the McAbs produced by the hybridoma lines were tested for specificity, only data from representative clones of each parental line are shown.

Monoclonal antibodies from representative hybridoma lines were also tested in indirect surface immunofluorescence assays (IFA) against mycelium from Sirococcus and the same commensal isolates. Although some of the McAbs recognized antigens exposed on the surface of Sirococcus mycelium (see below), none of the McAbs bound to mycelium of other fungal genera.

Morphological Distribution of Antigens Recognized by Sirococcus-Directed Monoclonal Antibodies.

Recognition of secreted antigens.--Monoclonals from representative hybridoma lines were tested in ELISAs in which ethanol-precipitated antigens from fungal culture medium (secreted antigens) were used to coat microplate wells. Several clones representing different parental hybridoma lines were tested. The data in table 3 show that two of the hybridoma lines (SDM 1/441.8.2 and SDM 1/171.27.13) produced McAbs which recognize antigen(s) that are also secreted into the culture medium by Sirococcus. No binding to

Table 2.--Reactivity of Sirococcus-directed monoclonal antibodies with soluble antigens from Sirococcus and other fungi

Fungus Genus[2]	A_{490} nm/Hybridoma[1] SDM 1/475.6a.5	SDM 1/441.4.4	SDM 1/434.15.21	SDM 1.171.27.22	SDM 2/392.2.4
Sirococcus	1.91	1.06	1.23	0.71	0.87
Trichoderma	0.05	0.14	0.04	0.10	0.03
Alternaria	0.04	0.05	0.03	0.04	0.03
Paecilomyces	0.05	0.05	0.05	0.11	0.04
Sclerophoma	0.03	0.03	0.02	0.03	0.02
Penicillium	0.04	0.04	0.04	0.07	0.03
Rhizopus	0.02	0.03	0.01	0.01	0.01
Mucor	0.02	0.02	0.02	0.02	0.01
Extraction Buffer	0.02	ND	0.01	0.02	0.04

[1] McAbs antibodies produced by SDM hybridomas were tested in ELISA using soluble antigens from S. strobilinus or from seven different fungal genera to coat microplate wells.

[2] Soluble antigens prepared from S. strobilinus and seven other fungal isolates from seedlot 2456 were coated onto ELISA microplate wells at a concentration of 10 µg protein/mL. Extraction buffer (see Methods) coated at 1/10 dilution served as a control.

secreted antigens of Penicillium was observed with any of the McAbs tested.

Recognition of surface antigens.--Monoclonals from representative hybridoma lines were tested in IFA for their ability to recognize antigens exposed on the surface of mycelium grown on MB. Pale yellow autofluorescence in mycelial preparations caused a background which interfered with interpretation of low levels of FITC (green) fluorescence due to specific

Table 3.--Reactivity of Sirococcus-directed monoclonal antibodies with fungal secreted antigens

SDM Hybridoma	A_{490} nm/Antigen[1] Sirococcus	Penicillium
1/434.15.21	0.08	0.05
1/171.27.13	2.00	0.07
1/441.8.20	0.68	0.05
1/475.6a.10	0.02	0.01
2/392.10.20	0.10	0.04

[1] Fungal secreted antigens were prepared by ethanol-precipitation of spent culture medium (see Methods).

antigen-antibody interactions. Therefore, the McAbs were tested several times in separate assays. Although the majority of the McAbs did not bind to the surface of Sirococcus, some McAbs produced two distinct patterns of fluorescence. Some McAbs produced bright patches of fluorescence at what resembled thin areas of the cell wall often near the hyphal tip or at broken ends of the hyphae ("patchy surface" fluorescence). Other McAbs produced bright punctuate fluorescence at structures resembling holes in the cell wall and on fibrillar material surrounding the hyphae ("patchy surface + fibrils"). These observations are summarized in table 4.

DISCUSSION

This paper has described the derivation by cell fusion techniques of monoclonal antibodies (McAbs) which recognize antigens of the fungus, S. strobilinus. This approach was necessary as preliminary investigations (unpublished) with polyclonal antisera raised in rabbits and mice by immunizing them with Sirococcus extracts revealed a considerable amount of cross-reactivity between Sirococcus and other nonrelated seed-associated fungi, presumably due to shared antigenic determinants. McAbs, which recognize a single site on an antigen molecule (Milstein 1980), may be selected for their ability to recognize unique antigenic sites in related organisms and therefore circumvent the problems of crossreactivity often observed with antisera. The Sirococcus-directed McAbs described herein did not recognize internal or surface antigens of nine different nonrelated fungi often associated with Sirococcus in seeds. Therefore, these McAbs are probably directed to unique antigens of S. strobilinus and will serve as useful diagnostic reagents for detecting this conifer pathogen in seeds or other tissues. These McAbs, as a group, also recognized antigens of eight other S. strobilinus isolates obtained from diverse host species and tissues. Therefore, the McAbs, although derived

Table 4.--Surface immunofluorescence patterns observed with Sirococcus-directed monoclonal antibodies

SDM Monoclonal Antibody	Fluorescence Distribution[1] Negative	Patchy Surface	Patchy Surface & Fibrils
1/441.4.2	● ●	● ●	
1/441.8.6	●		
1/441.8.18			●
1/171.21.16	● ●	●	
1/171.21.22		●	
1/434.15.9	● ●	●	
1/434.28.5	●		
1/475.6a.2	●		
1/475.6a.4		●	
2/392.5.31	●		● ●
2/392.2.4	● ●	●	
2/392.10.20		●	

[1] McAbs from representative SDM hybridoma cell lines were tested for surface binding to unit layers of Sirococcus strobilinus mycelium. Bound McAbs were detected with a mixture of FITC-conjugated goat anti-mouse IgM and goat anti-mouse IgG second antibodies at 1/20 dilutions. Each dot represents the results of one assay conducted with the monoclonal antibody.

using a single isolate, were not isolate-specific and can be used generally to detect this fungus. The observed differential patterns of reactivity of the monoclonals with other Sirococcus isolates suggest that they recognize more than one antigen and/or there is differential expression of these antigens in Sirococcus obtained from varied sources. Although all McAbs tested recognized antigens in isolates from spruce and pine hosts, only five hybridoma clones produced McAbs which recognized antigen(s) of Sirococcus isolated from western hemlock.

A preliminary characterization of the morphologic distribution of the antigens recognized by these McAbs indicated that some antigens may be exposed on the surface of the fungus and/or may be secreted into culture fluids. As mice were immunized with whole mycelium and therefore were exposed to the whole antigenic repertoire of the fungus, antibodies directed to both internal and surface antigens would have been generated. However, as antibodies produced by the hybridomas were selected in ELISA using only soluble antigens, a predominance of antibodies directed to internal components would be expected. Indeed, this was the case, as the majority of the McAbs did not react with the mycelial surface in IFA. However, several of the monoclonals exhibited a patchy distribution of surface fluorescence in these assays. Whether this represents reactivity of the McAbs with cell wall antigen(s) (that were also present in the soluble antigen preparation used in ELISA) or accessibility of the antibodies to an internal component through a lesion or thinning of the cell wall, is speculative. The variability in IFA fluorescence patterns may also reflect the age and physiologic state of the mycelial material used in the assays. Two monoclonals (SDM 1.172.27.13 and SDM 1/441.8.20) reacted in ELISA with Sirococcus secreted antigens. Another clone (SDM 1/441.8.18) produced antibody which reacted in IFA with both the mycelial surface and associated fibrillar material. Perhaps the antigens recognized by these McAbs may be enzymes or secondary metabolites that are transported to the exterior of the fungus.

The specificity of the Sirococcus-directed McAbs described here will allow their use as diagnostic probes for this pathogen in seeds and other plant tissues. Sensitive immunologic assays employing these McAbs are currently being developed with the objective of establishing a simple, rapid and accurate method for screening seedlots destined for use in forest nurseries or for export.

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IMPACT OF INSECTS ON SEED PRODUCTION IN A DOUGLAS-FIR SEED ORCHARD

Scott A. Dombrosky and Timothy D. Schowalter

ABSTRACT: The impact of various factors on seed production in a Douglas-fir (*Pseudotsuga menziesii*) seed orchard in western Oregon was examined by monitoring the fate of seeds in 30 cones, stratified into three crown levels, on each of 10 trees during the 1984 growing season. Cones were examined monthly between April and September for mortality or evidence of insect damage. In September a sample of mature cones was collected and completely dissected. Each seed was examined for extractability, insect damage, or unexplained abortion. These data were used to measure the relative impacts of various cone and seed mortality agents, and to develop an inventory monitoring system for management of Douglas-fir seed production. The results of this study indicate that, in addition to the recognized importance of insects to seed loss at cone maturity, insects also cause seed production losses through early conelet abortion in Douglas-fir.

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SELECTIVELY HARVESTING CONES WITH A FANDRICH AERIAL RAKE

Helmut Fandrich

ABSTRACT: Selecting the trees to be harvested from the air allows the forester to specify harvesting areas, elevations, type of trees and even specific trees. Aerially picking dominant trees at selected intervals with a Fandrich rake gives the forester the opportunity not only to freely specify the best trees from a broad genetic base, but also to rapidly collect large volumes during heavy crop years when the yields are higher and the costs are lower. The rate of picking can be estimated if one knows the quantity of cones near the top of the trees since the pilot will rake approximately one tree per minute.

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ASSESSING INDIVIDUAL SPECIES' IMPACT ON SEED YIELD AND COMMUNITY INTERACTIONS AMONG CONE AND SEED INSECTS

Nancy Rappaport

ABSTRACT: Methods are described for assessing individual species' impact on seed yield and community interactions among cone and seed insects. The procedure involves sequentially bagging cones to exclude all possible combinations of species. These exclusions may be viewed as a series of simulated pesticide applications. Thus, in our study, we excluded each of the three major pests of Douglas-fir cones singly and in combination with the other pest species. This was possible because there was a degree of nonoverlap in the oviposition phenologies of the principal pest species. Cones were left bagged during the oviposition periods of each species, then were exposed to allow oviposition by the other species. This permits assessment of impact by individual species and also yields information about potential associative and competitive interactions among the species. Such interactions may have important consequences for our pest management strategies, particularly if our treatments remove only certain of the pest species.

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USE OF SYSTEMIC INSECTICIDES TO PROTECT INDIVIDUAL TREES FROM WESTERN SPRUCE BUDWORM

Richard C. Reardon

ABSTRACT: Implantation and injection methods are described for protection of individual trees from western spruce budworm. Implantation is with Medicaps which contain a dry chemical; injection is with Mauget Systemic Injector Units which contain a liquid formulation. Impact of consecutive yearly applications in reducing western spruce budworm populations and in response of trees to wounding is described. The advantages and disadvantages of each method are compared.

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YIELD AND VIABILITY OF NORTHERN LODGEPOLE PINE SEED

Allen Richmond, John Alden, Thomas Malone, and Robert Van Veldhuizen

ABSTRACT: Lodgepole pine (*Pinus contorta* Dougl. ex Loud.) is the most widely planted conifer in boreal forests. Demand for seed from northern populations has accelerated cutting of trees for cone harvest. Populations from central Yukon are discontinuous and may not produce enough seed to meet demands unless utilization of cone crops is improved. At the present time, only cones from the 2- to 5-year age class are usually recommended for commercial collection.

Serotinous cones were found to contain viable seed to 55 years of age. Seed age had no effect on seed vigor as measured by rate of real (viable seed) germination. Seed recovery was not affected by age of cones. Seed viability declined with age, but still maintained relatively high germination rates to 20 years of age. The seed not collected in the 6- to 20-year age classes represents a wasted seed resource. Portions of this resource should be utilized as its viability and vigor are only slightly lower than seed from 2- to 5-year-old cones.

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DEFOLIATION AND DOUGLAS-FIR CONE AND SEED LOSSES CAUSED BY BUDWORM IN THE NORTHERN U.S. ROCKY MOUNTAINS

Raymond C. Shearer

ABSTRACT: In September 1979, counts of ovulate buds on 25 randomly selected branchlets on each of 22 Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) trees at 20 locations in the Northern U.S. Rockies predicted a good cone crop for 1980 throughout the study area. However, potential cone crop was nearly eliminated in areas of moderate to high defoliation by western spruce budworm (*Choristoneura occidentalis* Freeman), especially in Montana east of the Continental Divide and in nearby east-central Idaho. Few cones matured in stands with a 1980 defoliation-rating index greater than 40 percent. Stands with low to moderate defoliation-rating indexes (from 30 to 40 percent) had from 30 to 90 percent of the potential cones killed by budworm larvae. The remaining stands had low defoliation rating indexes (from 2 to 21 percent) and low cone mortality caused by budworm larvae (from 2 to 25 percent of the cone potential). Most of the mortality occurred during the early stages of cone development (92 percent were killed by budworm larvae in the bud or erect conelet stage). These losses accounted for about 80 percent of all seed mortality caused by budworm.

The remaining 20 percent of budworm-caused seed mortality occurred in mature cones. Budworm larvae reduced the number of viable seed in mature cones by 1 to 32 percent, depending on location. Seed loss in live cones increased in areas of greater defoliation. Other insects causing seed losses in mature cones were a cone moth (probably *Barbara colfaxiana* [Kearfott]), a cone worm (probably *Dioryctria* sp.), a scale midge (probably *Contarinia washingtonensis* Johnson), a seed chalcid (probably *Megastigmus spermotrophus* Wachtl), and a seedbug (probably *Leptoglossus occidentalis* Heidemann).

Forest managers should not depend on Douglas-fir cones to provide seed for artificial or natural regeneration when the stand-defoliation index is greater than 30 percent, even in years of potentially heavy cone production. Budworm larvae also decrease seed production in stands with defoliation under 30 percent. To protect Douglas-fir cone crops, insecticide should be applied when the cone and pollen buds open.

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REDUCING DOUGLAS-FIR SEED AND CONE DAMAGE

Lawrence E. Stipe

During 1979 and 1980, single, double, and triple ground applications of acephate and carbaryl were used to improve Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) seed and cone production in areas of moderate to heavy western spruce budworm (*Choristoneura occidentalis* Freeman) populations. Ten single-tree replications were used for all treatments. Cone-bearing Douglas-fir trees 9 to 18 m (30 to 60 ft) tall were selected by examining cone buds, then randomly assigned one of the three treatments. Mixing and application rates were according to label instructions: acephate--400 g (300 g Al) in 500 L water (2/3 lb. [1/2 lb. Al] in 100 gal. water); and carbaryl--2.5 L (1.2 kg Al) in 500 L water (2 qt. [1 lb. Al] in 100 gal. water).

Each tree was sprayed beyond the point of runoff with a hydraulic pumper and handgun operated at 28 kg/cm^2 (400 lb/in^2). The single application, timed to coincide with peak second instar spring dispersal, was on May 21, 1979, when cone buds had expanded to 2.54 cm (1 in) long and were still erect. Postspray densities of fourth instars for acephate, carbaryl, and control were 3.6, 1.3, and 21.2 larvae per 100 shoots, respectively; defoliations after pupation were 10.8, 2.2, and 73.0 percent, respectively. Of the potential 68 seeds per cone, the single application provided seed production per cone of 0.5 seed for acephate, 1.0 seed for carbaryl, and no seeds for control. These less-than-expected results were primarily because budworm feeding had damaged over 30 percent of the cones before treatment and because subsequent cone damage by budworm and other seed-and-cone species had caused additional damage before cone harvest on August 23. To reduce prespray infestation losses and provide longer protection, double and triple applications were tested the next year. The first applications were on May 8 and 9, 1980, coinciding with the beginning of larval dispersal, which peaked on May 24. This earlier timing reduced prespray cone damage to less than 14 percent. The second applications were on May 27 and 28. The last of the triple application was on June 16. Postspray, mature budworm larvae per 100 shoots for acephate, carbaryl, and control were 0.9, 0.6, and 16.3 for double application and 0.3, 0, and 16.3 for triple application; defoliation was 4.8, 0.9, and 77.5 percent for single application, 1.1, 0.6, and 77.5 percent for double application, and 1.3, 0.6, and 77.5 percent for triple application. Mature cones were collected on August 18. Total seed yield for acephate, carbaryl, and control was 34.2, 41.4, and 22.5. Total seed yield for all spray treatments was significantly different from the control, but no significant differences were found between acephate and carbaryl or between double or triple applications. Seed condition (sound, hollow, and insect-damaged) and germination differences were small, variable, and not related to treatment. Where seed yields are important and budworm populations are moderate to heavy, a double application of either acephate or carbaryl is recommended. Time the first application when budworm larvae first begin spring dispersal, and follow with a second in about 14 days.

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SYMPOSIUM SUMMARY: CONIFER TREE SEED IN THE INLAND MOUNTAIN WEST

Stanley L. Krugman

In spite of the recent advances in tree propagation, such as tissue culture and mass rooting, seeds will remain the major source of planting material for many years to come. Each year we are dealing with more tree species from more areas. Each year we are working with a larger number and variety of seed lots as we attempt to better match seed source to site. As the genetics and tree improvement programs expand there is a continuous need for additional information including time of flowering, and improved methods of collecting, processing, storing, and germinating seeds.

Basically such information is needed to improve efficiency and to reduce field planting costs. Speakers throughout this meeting have addressed these issues from a number of different points of view. We have been fortunate to have researchers as well as regeneration specialists share their experiences with us. Predicting and stimulating seed production remains a major issue in western forestry. A further understanding of flowering biology and development is essential if a rational program is to be initiated. The review of cone and seed biology and development by John N. Owens demonstrated that there are a series of critical stages in cone and seed development. We need to have an understanding of them for our individual species under our local environmental conditions if we are to obtain maximum yield or at least reduce certain types of losses. Closely related is the use of hormones to stimulate flowering in some of our western species. Stephen D. Ross reviewed the current experience with hormones, their value, and limitations. Although the system is not perfect, for selected species and purposes we now have a valuable tool. Reports by Glenn L. Jacobsen, Allen S. Rowley, and Raymond C. Shearer pointed out that many conditions influence cone production and seed yield and our understanding of environmental influences is still very primitive. Interesting papers by Katherine A. Yakimchuk, R. J. Hoff, Carole L. Leadem, and A. K. Hellum provide new data on seed germination and methods for increasing germination. These papers and several others, however, demonstrated we are not consistent in defining germination. As noted by Katherine A. Yakimchuk, we need to consider both radicle elongation and seedling development. This is an important element since older seeds and immature seeds, as well as damaged seeds, when germinated may have radicle elongation but seedling development is abnormal and the resulting seedlings will perish in the nursery bed.

Biotechnology that offers unique opportunities in tree improvement may soon play a major role in reducing seedborne diseases. The research by Leslie Ann Mitchell suggests that the further development of appropriate monoclonal antibodies techniques will be a valuable tool in recognizing seedborne fungal pathogens. More traditional and nontraditional approaches to disease and insect protection were discussed by Michael I. Haverty, Patrick J. Shea, William F. Johns, and Richard C. Reardon. Although the methods are promising, most such techniques can only be used in high-value areas such as seed orchards or superior seed stands. As we increase our seed crops annually through manipulations we can expect an increase in disease and insect problems; improved protection techniques are badly needed.

A major value of this meeting, in addition to the sharing of current information and experiences, is that it brought the researchers and practitioners together. For the nurserymen and nurserywomen I would suggest that some of the problems raised by your papers and questions have already been answered by earlier research. It would appear to me that we still have an information gap. For the scientists in the audience I would like to once again state that your job does not end with the publication of a scientific paper but must include at least an attempt to translate the science into useful and, if possible, practical methods for the field user. To encourage such activities we need to in the future, as we did here, bring the field user groups and the scientists together in common meetings. I believe we all found the meeting of use and I look forward to the published proceedings.

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Includes six reviews and 34 papers presented in four technical sessions: cone and seed biology; cone prediction, collection, and processing; seed orchard and seed production area management; and effects of vertebrates, insects, and diseases on seed production. Current information is presented on conifer tree cones and seeds native to the Inland Mountain West (east slopes of the coastal ranges to the plains of the United States and Canada).

KEYWORDS: conifers, cone and seed biology, seed orchards, seed production area, cone and seed damage

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This publication reports research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All uses of pesticides must be registered by appropriate State and/or Federal agencies before they can be recommended.

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